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SYSTEMATICS, DISTRIBUTION, AND BIOLOGY OF CEPHALOPODS OF THE GENUS *TREMOCTOPUS* (OCTOPODA: TREMOCTOPODIDAE)

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ABSTRACT

The octopods of the genus *Tremoctopus* are reviewed on a world-wide basis. Two species are recognized: *T. violaceus* and *T. gelatus*, n. sp. *Tremoctopus violaceus* is separated into two subspecies *T. v. violaceus* in the Atlantic and *T. v. gracilis* in the Indo-Pacific. Each species and subspecies is fully described and the status of the nominal species is clarified.

A morphometric analysis is given for *T. violaceus violaceus*. Geographical and vertical distribution, associations with other animals, behavior, and reproduction also are discussed.

While the typical octopod, as represented by *Octopus*, is a benthic animal of shallow waters, species of about 10 genera (excluding the finned octopods) are pelagic. Three of these genera, one of which is *Tremoctopus* Delle Chiaje, 1830, belong to monotypic families.

As these three epipelagic families (Argonautidae, Ocythoidae, and Tremoctopodidae) share certain morphological similarities, Robson (1932) grouped them under the single tribe, Argonautida, characterized by marked sexual dimorphism. The sexual dimorphism, as well as the reproductive adaptations that have evolved, present many interesting problems for study.

Males of these three genera all have a detachable hectocotylized arm which serves as a means of storage and transfer of the spermatophores (Robson, 1932). The hectocotylus, a complex structure with some unusual modifications, provide one of the basic criteria for specific and subspecific determination in *Tremoctopus*.

Tremoctopus is distinguished by two pairs of conspicuous pores, one pair ventral and adjacent to the funnel and another pair on the dorsal surface of the head between the eyes. These pores open into a cephalic canal system, the function of which is still unknown. The only other cephalopod known to possess pores is *Ocythoe*, which has one ventral pair.

The high degree of allometric growth which occurs during development results in marked changes of bodily proportions with increasing age of the animal. Most past descriptions of new species have been based on a limited number of immature specimens. This has led to an extensive series of nominal species, most of which represent growth stages of *T. violaceus*.

The present treatment of the genus describes the peculiar morphological changes occurring in these animals and clarifies their confused systematic status.

Historical Review

Stephani Delle Chiaje (1830) described the genus *Tremoctopus*. The plates, Figures lxx and lxxi, depict a large female bearing the name *Tremoctopus violaceus*. The web configuration, arm proportions and aquiferous pores, although drawn in a somewhat stylized manner, are clearly recognizable.

In 1835 d'Orbigny described a number of pelagic octopods which he grouped under the name *Philonexis*, a subgenus of *Octopus*. He later (1838) raised *Philonexis* to generic rank. This genus included those pelagic forms with unequal arms (an arm formula generally of 2.1.4.3), an extensive web be-

tween the first two pairs of arms and water pores on the head.

Eydoux and Souleyet (1852) described two species of *Octopus*, *O. gracilis* and *O. dubius*, (1852) described two species of *Octopus*, *O. gracilis* and *O. dubius*, that appear to belong to *Tremoctopus*. Their descriptions, however, were poor and the true identity of *O. dubius* is doubtful.

Tryon (1879) placed Delle Chiaje's *T. violaceus* in a new family, Tremoctopodidae (as Tremoctopidae) and placed *Philonexis* in synonymy under *Tremoctopus*.

In 1895, Joubin described a new species, *Tremoctopus hirondellei*, based on a very young, single specimen with a total length of 9 mm. It was distinguished from the other species by short and subequal arms, a small head and inconspicuous eyes.

Jatta (1896) gave a comprehensive description of the males and females of *T. violaceus* which led him to believe that *T. violaceus* was the valid species of the genus. He suspected that all the other nominal species probably represented stages in the development of *T. violaceus*.

Berry (1912) listed *T. gracilis* and *T. quoyanus* as synonyms of *T. violaceus*. He considered his female specimens, about 58 mm in maximum total length, to be mature adults. Although he essentially followed Jatta's opinion and called his specimens *T. violaceus*, he felt that further study might prove his specimens to belong to the similar species, *T. gracilis*.

Naef (1923) published the most comprehensive developmental study of *T. violaceus*. He characterized the species and described and illustrated a series of growth stages depicting the changing proportions of the body, head and arms.

Naef recognized the peculiar ontogeny of both the funnel organ and the dorsal arms. He also observed the presence of coelenterate tentacle fragments on the dorsal and dorso-lateral arms of young animals. In 1928, he continued his study of *Tremoctopus violaceus*, this time dealing with its embryology and drawing comparisons with the closely related argonautids.

Robson (1932) reviewed the genus, summarized the literature, and discussed the possible synonymies. On the status of earlier species he remarked, "I have retained as distinct species *T. violaceus*, *microstoma*, *gracilis*, *dubius*, *ocellatus*, *hirondellei* and *scalenus*, though all but the first named seem to me to be of doubtful position. All the other forms I have no option but to treat as *T. violaceus*."

In 1963, Akimushkin reported on a collection of small *Tremoctopus* from the West Pacific, stated to exhibit bioluminescence. He noted that the females possessed spherical organs on the dorsal arms and concluded that they functioned as photophores and thus named the species *T. lucifer*.

Methods and Materials

All specimens were collected at sea or obtained from strandings on Florida beaches. Animals obtained by the writer were fixed in 10% buffered formalin and transferred to 70% ethyl alcohol. Loan specimens were stored in ethyl alcohol, isopropyl alcohol, or formalin.

Tissue from the dorsal arms of young females and the glandular bodies in the web of adult females were embedded in paraffin, sectioned at 8 μm and stained with hematoxylin and eosin.

The young of *Tremoctopus* were commonly found to have fragments of coelenterate (*Physalia*) tentacles attached to their dorsal and dorso-lateral arms. These fragments were identified by C. E. Lane. Stomach contents of preserved animals were examined and identified where possible.

The majority of the measurements used in this paper are from Voss (1963). All measurements are given in mm. The following new abbreviations are used throughout the text:

PL—Pore Length: The antero-posterior length of the cephalic water pores. The measurement is given separately for the dor-

sal (PL_d) and ventral (PL_v) pores. It is always the length of the longer pore of the pair.

PLI—Pore Length Index: The length of the longer pore of either the dorsal (PLI_d) or the ventral (PLI_v) pair as a percentage of the mantle length.

The following abbreviations for the source or deposition of the material are used: CASIZ, California Academy of Science, Museum of Invertebrate Zoology, San Francisco, California; NMFS, National Marine Fisheries Service, Hawaii; OM, Oslo Museum, Norway; SAM, South African Museum, Cape Town, South Africa; SIO, Scripps Institute of Oceanography; TRFRL, Tokai Regional Fisheries Research Laboratory, Tokyo, Japan; UMML, University of Miami, Marine Invertebrate Museum; and USNM, Catalogue designation for the National Museum of Natural History.

SYSTEMATICS

Family TREMOCTOPODIDAE Tryon, 1879 (emend.)

Philonexidae d'Orbigny, 1840: 159.—Gray, 1849: 24 (pars).—Adams, H. and Adams, A., 1858: 21. —Verrill, 1882: 388 (pars).—Hoyle, 1886: 214. —Ortmann, 1888: 642.—Carus, 1890: 458.—Joubin, 1895: 10.—Jatta, 1896: 202.—Joubin, 1900: 27.—Chun, 1914: 18, 1915: 478.—Joubin, 1920: 30.—Akimushkin, 1963: 152.

Tremoctopodidae Tryon, 1879 (emend.): 130.—Brock, 1882: 589.—Fischer, 1882: 334 (pars).—Hoyle, 1904: 12.—Berry, 1920: 156.—Adam, 1937: 80, 1942: 17.—Dell, 1952: 71.—Adam, 1954: 188.—Voss, 1956: 170.—Akimushkin, 1963: 152.—Voss, 1967: 86.—Voss and Williamson, 1971: 110.

Argonautidae Tryon, 1879: 133.—Naef, 1912: 198.—Degner, 1925: 80.—Sasaki, 1929: 19.

Diagnosis.—Extreme size sexual dimorphism; two pairs of cephalic water pores, one dorsal and one ventral, on the head; funnel organ with numerous longitudinal folds in adult females, W-shaped in very young females and in males; arm formula 1.2.4.3. or 2.1.4.3.; arms 1 characteristically truncated in adult females; sectors A and B of web extensive in females. Third right arm of male hectocotylized, developed in a sac.

Type-genus.—*Tremoctopus* Delle Chiaje, 1830, pls. lxx, lxxi.

Genus *Tremoctopus* Delle Chiaje, 1830

Tremoctopus Delle Chiaje, 1830: pls. lxx, lxxi; 1841: 6.—Gray, 1849: 27.—Steenstrup, 1860: 332.—Keferstein, 1866: 144.—Woodward, 1871: 164.—Tryon, 1879: 130.—Kolliker, 1844: 161, 1849: 67.—Targione Tozzetti, 1869: 591.—Tiberi, 1880: 14.—Brock, 1880: 210, 1882: 589. —Ninni, 1885: 161.—Hoyle, 1886: 67.—Ortmann, 1888: 642.—Carus, 1890: 458.—Joubin, 1893: 218.—Pelseneer, 1894: 207.—Jatta, 1896: 203.—Hoyle, 1909: 258.—Berry, 1912: 281.—Naef, 1912: 199.—Chun, 1915: 478.—Joubin, 1920: 30.—Naef, 1921: 537, 1928: 299.—Sasaki, 1929: 29.—Robson, 1932: 206.—Joubin, 1937: 39.—Adam, 1942: 17.—Benham, 1944: 294.—Saccarao, 1949: 5, 1951: 98.—Dell, 1952: 71.—Adam, 1954: 188.—Voss, 1956: 170.—Rees and Maul, 1956: 274.—Jones, 1963: 764.—Akimushkin, 1963: 164.—Voss, 1967: 86.—Rancurel, 1970: 70.—Voss and Williamson, 1971: 110.

Octopus d'Orbigny, 1835: 17.—Owen, 1836: 111. —Rang, 1837: 60.—Ferussac, 1835: pls. 18–20. —Philippi, 1844: 201.—Verany, 1851: 33.—Eydoux and Souleyet, 1852: 13.

Philonexis d'Orbigny, 1840: 83 (pars).—Gray, 1849: 24 (pars).—Gray, 1849: 24 (pars).—Troschel, 1857: 44.—Arango y Molina, 1878: 146.

Diagnosis.—With the characters of the family.

Type-species.—*Tremoctopus violaceus* Delle Chiaje, 1830: pls. lxx, lxxi. By monotypy.

KEY TO THE SPECIES AND SUBSPECIES OF *Tremoctopus* BASED UPON ADULT CHARACTERS

1a. Body gelatinous, transparent; light reddish brown in color; 8–11 gill filaments in females, 7–8 in males .... *T. gelatus* n. sp.
1b. Body firm muscular; blue-purple dorsally, gold ventrally; 13–16 gill lamellae in females, 9–11 in males 2a
2a. 15–19 pairs of suckers on distal portion of hectocotylus, 22–23 pairs on proximal portion of hectocotylus. Atlantic Ocean and Mediterranean Sea .... *T. violaceus violaceus*
2b. 19–22 pairs of suckers on distal portion of hectocotylus, 27–29 pairs on proximal portion of hectocotylus. Pacific and Indian Oceans .... *T. violaceus gracilis*

Tremoctopus violaceus violaceus Delle Chiaje, 1830
Figures 1–9 and 13–17

Tremoctopus violaceus Delle Chiaje, 1830: pls. lxx, lxxi, 1841: 6.—Gray, 1849: 27.—Keferstein, 1866: 144.—Targione Tozzetti, 1869: 591.—

Tryon, 1879: 130.—Tiberi, 1880: 14.—Brock, 1880: 214, 1882: 583.—Ninni, 1885: 161.—Steenstrup, 1860: 332.—Fischer, 1882: 335.—Carus, 1890: 458.—Hoyle, 1886: 214.—?Colombatovic, 1889: 7.—Jatta, 1896: 204.—LoBianco, 1909: 656.—Naef, 1912: 198, 1916: 17.—Massy, 1916: 144.—Joubin, 1920: 30.—Naef, 1921: 538, 1923: 735.—Degner, 1925: 80.—d'Aguilar-Amat, 1926: 140.—Neviani, 1927: 200.—Naef, 1928: 299.—Robson, 1932: 206 (pars).—Joubin, 1937: 39.—Adam, 1937: 80.—Saccarao, 1951: 98.—Salisbury, 1953: 40.—Adam, 1954: 188.—Voss, 1956: 170.—Rees and Maul, 1956: 274.—Voss, 1967: 86 (pars).

Octopus microstomus Reynaud, 1830.

Octopus velifer Ferussac, 1835: pls. 18, 19.—Phillippi, 1844: 201.

Octopus violaceus Ferussac, 1835: pl. 20.—Verany, 1851: 41.

Octopus atlanticus d'Orbigny, 1835: 19.

Octopus quoyanus d'Orbigny, 1835: 17.

Octopus semipalmatus Owen, 1836: 112.

?*Octopus hyalinus* Rang, 1837: 66.

Octopus velatus Rang, 1837: 60.

Philonexis velifer, d'Orbigny, 1840: 91.

Philonexis quoyanus, d'Orbigny, 1840: 96.—Arango y Molina, 1878: 146.

Philonexis atlanticus d'Orbigny, 1840: 98.

Philonexis microstomus, d'Orbigny, 1840: 100.—Troschel, 1857: 44.

?*Philonexis hyalinus*, d'Orbigny, 1840: 205.

Tremoctopus quoyanus, Gray, 1849: 27.—Kolliker, 1849: 67.—Tryon, 1879: 131.—Hoyle, 1886a: 70 (pars), 1886b: 214 (pars).—Jatta, 1889: 63.—Hoyle, 1912: 276.—Robson, 1932: 212.—Steenstrup, 1860: 332.

Octopus koellikeri Verany, 1851: 33.

?*Tremoctopus hyalinus*, Tryon, 1879: 131.—Hoyle, 1886b: 215.—?Chun, 1915: 478.

?*Tremoctopus hirondellei*, Joubin, 1895: 10. not *Tremoctopus hyalinus*, Joubin, 1900: 27.

Tremoctopus atlanticus, Tryon, 1879: 130.—Hoyle, 1886a: 71, 1886b: 214.—Chun, 1914: 18.

Tremoctopus microstomus, Tryon, 1879: 130.—Hoyle, 1886b: 215.—Carus, 1890: 457.—Robson, 1932: 214.

Tremoctopus ocellatus Brock, 1882: 601.—Hoyle, 1886b: 215.

Tremoctopus microstoma, Joubin, 1893: 218.

Material Examined.—95 males and 126 females from the following stations and localities.—1♀, ML 82.5 mm, Crandon Park Beach, Miami, Florida, J. Banta, 27 January 1971, surface, in collector's possession.—1♀, ML 47.8 mm, Quarantine ship, off Miami Beach, Florida, 30 January 1948, surface, UMML 31.10.—3♀♀, ML 6.6–25.2 mm, 1♂, ML 7.7 mm, Oregon Sta. 1305, 27°18′N, 89°25′W, 5 June 1955, 0–1305 M, UMML 31.455.—1♀, ML 16.8 mm, Combat Sta. 371, 35°07′N, 75°13′W, 16 June 1957, surface, UMML 31.148.—1♀, ML 10.4 mm, Discoverer Cr. 425E, Atex Drift Program, 12°39′N, 40°57′W, 11–12 February 1969, surface, UMML 31.666.—1♂, ML 10.5 mm, Oregon Sta. 2945, 28°33′N, 88°48′W, 25 August 1960, 100–125 fms, UMML 31.270.—3♀♀, ML 12.1–12.8 mm, 1♂, ML 9.2 mm, Discoverer Cr. 425E, Atex Drift Program, 12°57′N, 40°09′W, 8 February 1969, surface, UMML 31.671.—1♀, ML 12.6 mm, Discoverer Cr. 425E, Atex Drift Program, 13°07′N, 39°45′W, 8 February 1969, surface, UMML 31.668.—1♂, ML 11.9 mm, Oregon Sta. 1298, 26°30′N, 89°15′W, 30 April 1955, UMML 31.1109.—4♀♀, ML 6.8–9.3 mm, 2♂♂, ML 10.5–10.6 mm, Silver Bay Sta. 4705, 25°44′N, 76°16′W, 6 March 1963, UMML 31.1100.—1♀, ML 9.3 mm, Discoverer Cr. 425E, Atex Drift Program, 12°27′N, 41°21′W, 11–12 February 1969, surface, UMML 31.667.—8♀♀, ML 6.6–10.8 mm, 2♂♂, ML 9.0–10.3 mm, Discoverer Cr. 425E, Atex Drift Program, 13°27′N, 39°30′W, 7–8 February 1969, surface, UMML 31.669.—27♀♀, ML 7.0–15.9 mm, 26♂♂, ML 5.6–13.0 mm, Discoverer Cr. 425E, Atex Drift Program, 13°49′N, 39°03′W, 5–6 February 1969, surface, UMML 31.670.—49♀♀, ML 5.6–17.9 mm, 36♂♂, ML 6.1–13.8 mm, Discoverer Cr. 425E, Atex Drift Program, 13°43′N, 38°58′W, 6–7 February 1969, surface, UMML 31.1062.—1♂, ML 10.5 mm, Oregon Sta. 1035, 26°40′N, 92°00′W, 8 May 1954, UMML 31.456.—1♀, ML 105 mm, Sewage Disposal Beach, Virginia Key, Miami, Florida, D. Tabb, 27 October 1960, stranded, UMML 31.244.—1♀, ML 15.2 mm, Delaware Sta. 19, 30°13.2′N, 53°21′W, 22–23 May 1963, surface, UMML 31.1070.—1♀, ML 12.6 mm, Delaware Sta. 25, off Bermuda, 26–27 May 1963, surface, UMML 31.1069, 1♀, ML 9.9 mm, Oregon Sta. 1357, 28°47′N, 87°50′W, 10–11 August 1955, surface, UMML 31.1103.—1♀, ML 190 mm, Virginia Key, Miami, Florida, R. Thomas, 13 April, 1971, stranded, UMML 31.1104.—2♀♀, ML 189–192 mm, Key Biscayne, Miami, Florida, J. Espy, 13 April 1971, stranded, UMML 31.1105.—3♂♂, ML 6.4–6.5 mm, Undaunted Cr. 1966-3, Sta. 2, 32°44′N, 65°00′W, 6 May 1966, surface, UMML 31.1067.—1♂, ML 5.6 mm, Undaunted Cr. 1966-3, Sta. 14, 32°33′N, 64°50′W, 9 May 1966, surface, UMML 31.1065.—4♀♀, ML 6.2–8.9 mm, 9♂♂, ML 5.2–11.8 mm, Undaunted Cr. 1966-3, Sta. 25, 30°04′N, 75°50′W, 13 May 1966, surface, UMML 31.1066.—1♂, ML 150 mm, Crandon Park Beach, Key Biscayne, Miami, Florida, J. Espy, 5 April 1971, stranded, UMML 31.1106.—1♀, ML 162 mm, Key Biscayne, Miami, Florida, J. Espy, 13 April 1971, stranded, UMML 31.1107.—3♂♂, ML 11.2–13.8 mm, Discoverer Cr. 425E, Atex Drift Program, 13°49′N, 39°03′W, 5–6 February 1969, surface, UMML 31.1063.—1♂, ML 153 mm, Key Biscayne, Miami, Florida, K. Langford, 5 December 1961, stranded, UMML 31.179.—1♀, ML 255 mm, Virginia Key, Miami, Florida, 1960, stranded, UMML 31.361.—1♀, ML 151 mm, Miami, Florida, UMML.—1♀, ML 250 mm, Miami, Florida, UMML.—1♀, ML 197 mm, Miami, Florida, UMML.—1♀, ML 182 mm, Key Biscayne, Miami, Florida, W. Stephens, 14 April 1968, stranded, UMML.—1♀, ML 122 mm, Crandon Park Beach, Miami, Florida, Hubbell, 7 April 1966,

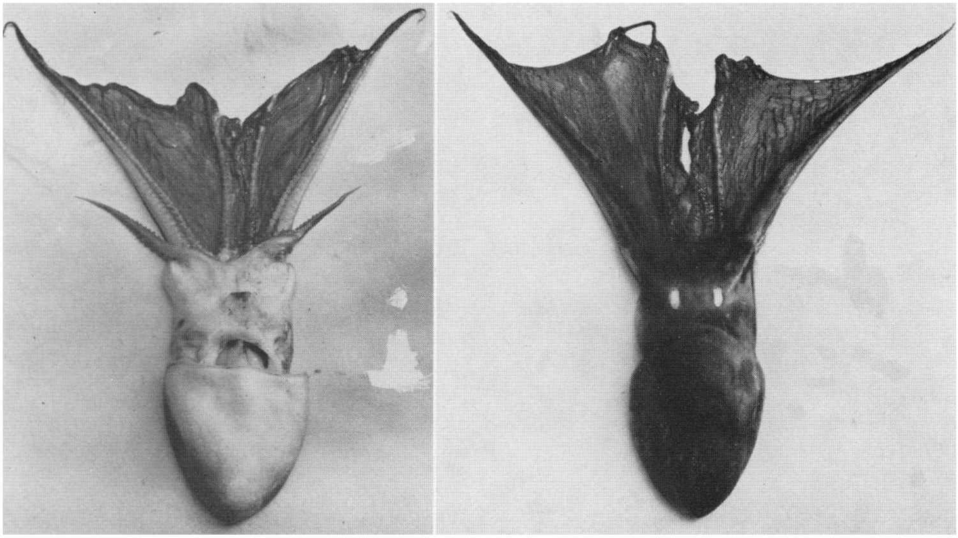


Figure 1. *Tremoctopus violaceus violaceus,* adult females. a, dorsal view; b, ventral view.

stranded, UMML.—1 ♀, ML 107 mm, Crandon Park Beach, Miami, Florida, J. Banta, 10 October 1971, stranded, UMML.—1 ♀, ML 162 mm, 5 miles east of Turtle Reef, Captain Heldin, April 1962, 31.412.—1 ♀, ML 154 mm, Fort Lauderdale, Florida, 6 April 1960, stranded, UMML 31.9.—1 ♀, ML 119 mm, Crandon Park Beach, Miami, Florida, 15 April 1958, stranded, UMML 31.173.—1 ♀, ML 11.6 mm 1 ♂, ML 11.9 mm, PILLSBURY Sta. 1167, 19°50′N, 66°19′W, 20 January 1970, surface, UMML 31.1097.—1 ♀, ML 4.6 mm, PILLSBURY Sta. 817, 19°38.5′N, 67°19′W, 29 January 1969, UMML 31.1098.—beaks, Fort Lauderdale, Florida, January 1950, UMML 31.117.—1 ♂, ML 7.2 mm, OREGON Sta. 5014, 12°43′N, 59°22′W, 17 September 1964, surface, UMML 31.1101.—1 ♂, ML 4.9 mm, UNDAUNTED Cr. 1966-3, Sta. 8, 32°36′N, 65°00′W, 7 May 1966, surface, UMML 31.1068.

Diagnosis.—Mantle of females bluish-purple on dorsum and silvery gold on ventrum, males with few scattered chromatophores and lighter in color; mantle firm, muscular; 13–16 gill filaments on outer demibranch of females, 9–11 in males; distal portion of hectocotylus with 15–19 pairs of suckers proximal with 22–23 pairs.

Description of the Females

Adults.—Females (Fig. 1) reach a total length of about 1 m. In life the dorsal surface of the body and head is dark bluish-purple; the ventral surface is an iridescent silvery gold color. The web is deep maroon.

The mantle is smooth, thick and muscular. Its shape depends on the size of the animals. In animals 100–200 mm in length, the mantle width index is about 60–70. The mantle tapers to a very blunt point posteriorly.

There are two dorsal stylets embedded in the mantle at the base of the funnel retractor muscles. The stylets, transparent, with a reddish coloration along the central axis, are stout straight rods (Fig 4h) measuring 5.5 × 25.4 mm in the adult female examined.

The head is narrower than the mantle, constricted in the neck region and bears large laterally-directed eyes. There are about 8–10 nuchal folds posterior to the eyes.

There are two pairs of oval "aquiferous pores" (Fig. 1). One pair opens on the dorsal surface of the head between and slightly anterior to the eyes. The second pair opens on the ventral surface of the head adjacent to the opening of the funnel. The dorsal pores ($PL1_d$: 2.7–8.4–17.7) are usually larger than the ventral ones. Their function is unknown.

The arms are unequal in size and shape (Fig. 1). The arm order is typically 2.1.4.3. or 1.2.4.3. The suckers are biserial and elevated on broad bases. Arms I are truncated in adults and the segment of the arm proximal to the truncation is degenerate. The suckers decrease in size toward the end of the arm and become widely set apart in an alternating arrangement. Arms II are stout and flattened along the oral surface. The suckers (Fig. 4f) are degenerate in adults and appear along much of the arm as two rows of inconspicuous lateral projections. Arms III and IV exhibit no unusual modifications. Their biserial suckers (Fig. 4g) gradually decrease in size distally.

The web is well developed with the formula B.A.E.C.D. Sector A is deep; it extends to the tip of the truncated arms and medially has a V-shaped cleft. Along the edge of the web parallel to the arm is a row of "pouches," which may play a role in the attachment of the egg clusters to the web (Portmann, 1952). Histological sections revealed a secretory function for the cells of the pouches. The web extends to the tips of the arms II. Pouches are also found in sector B. Most adult females are from beach strandings so the web is usually damaged to some degree. Also, the animals apparently are able to autotomize portions of the web along visible fracture lines (Kramer, 1937). Thus, depending on the condition of the web, these pouches may not be present.

The funnel is moderate in size, extends beyond the level of the eyes, and is free for about ¼ of its length. The funnel-mantle locking apparatus (Fig. 4, d, e) consists of a rigid recurved portion of the posterior margin of the funnel which articulates with a depression in the mantle wall. The funnel organ (Fig. 5c) is W-shaped with a series of longitudinally oriented parallel folds of glandular tissue in adults; it exhibits a marked alteration in appearance during growth.

The gills contain 13–16 gill filaments on the outer demibranch. The number of gill filaments is consistent in females ranging from 5.6–255 mm in mantle length.

The buccal mass (Fig. 5f) is large and contains two large anterior salivary glands. The posterior salivary glands (Fig. 5f) are small and triangular. A fine duct passes from each posterior gland; these unite forming a single duct which passes into the posterior region of the buccal mass.

The radula (Fig. 4c) has nine teeth in each transverse row. The central (rachidian) tooth exhibits an A_2 seriation. It is tricuspate, with the lateral cusps about ¾ the length of the median cusp. The first lateral is small, at about a 45° angle to the rachidian, and with one strongly curved cusp. The second lateral is large with a single cusp. The third lateral is long, slender, spine-shaped. The marginal plate is thin and rectangular. In the specimens observed, the radula appeared constant in tooth shape and in the number of teeth per row. One specimen, however, lacked first lateral teeth.

The slender esophagus (Fig. 5f) enlarges into a well-developed crop leading to a muscular stomach (Fig. 5f). The spiral caecum is large; the intestine passes between the two hepato-pancreatic ducts joining the liver, pancreas and spiral caecum. The thin intestine proceeds without major modifications (except for a dilation near the caecum) to the anus which has two long anal flaps.

A prominent ink sac (Fig. 5f), embedded in the ventral surface of the liver, gives off a short duct that opens into the intestine immediately prior to the anus.

A short thin duct arises from the saccular (Fig. 5g) and bifurcates to form the two proximal oviducts. These lead into the small, muscular, oviducal glands. The oviduct dilates anterior to the oviducal gland and then narrows again to a slender distal oviduct. There is a second conspicuous enlargement near the opening. Apparently mature eggs are oval and measure 2.9 × 1.8 mm exclusive of the stalk.

Larvae and Juveniles.—Both the head and mantle are wide (MWI and HWI may be

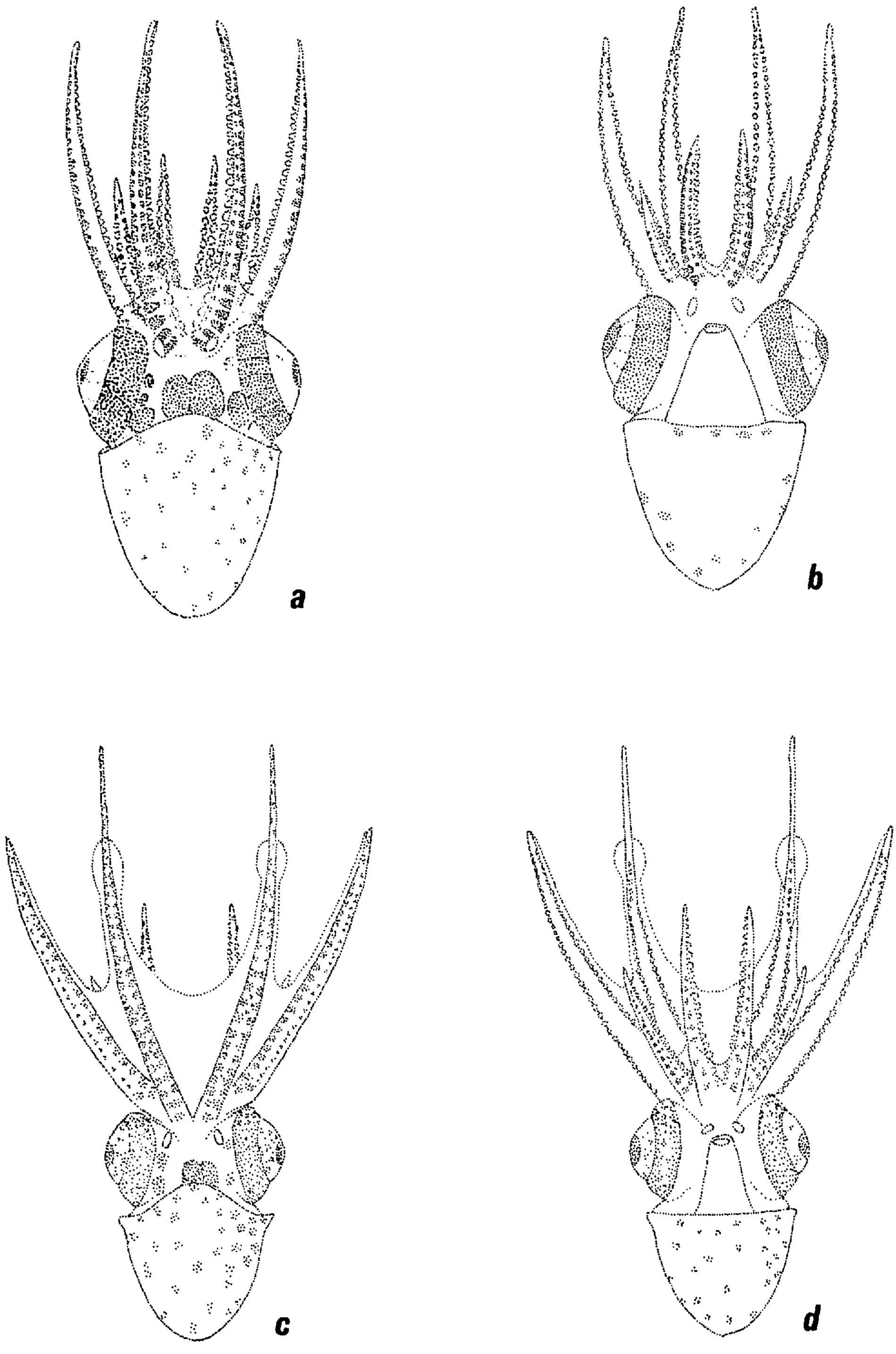
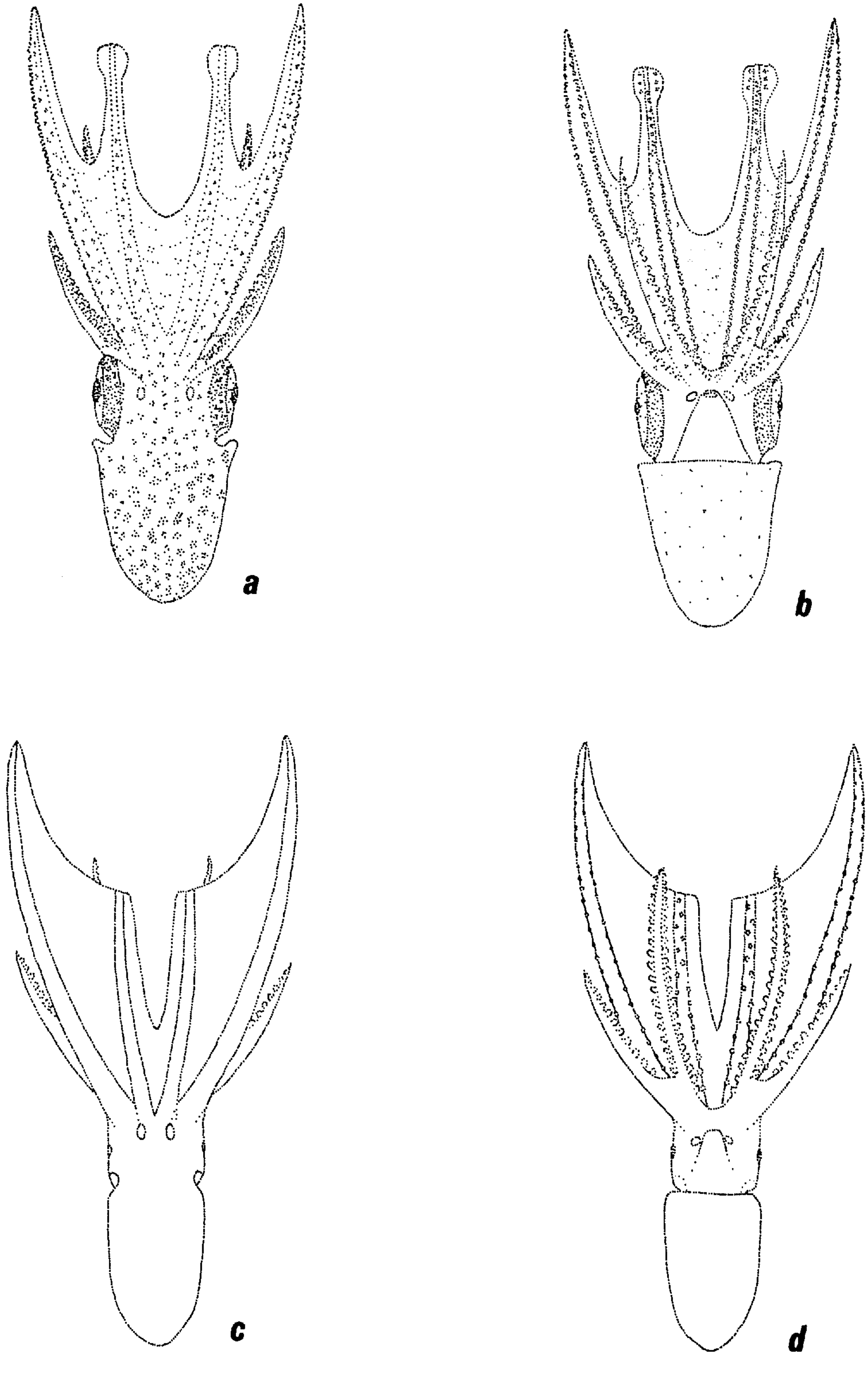


Figure 2. *T. violaceus violaceus*, females. a–b. ML 6.7 mm; a, dorsal view; b, ventral view; c–d. ML 10.1 mm; c, dorsal view; d, ventral view.


a
b
c
d

greater than 100). The eyes are large and in young animals are directed anteriorly (Fig. 2, a, b). If the tissue surrounding the eye is torn, the eye may appear to be stalked. The water pores are clearly seen in larve with a mantle length of about 6–10 mm (Fig. 2).

Chromatophores are poorly developed except along the anterior border of the mantle and on the dorsal surface of the head (Figs. 2, 3).

The arm order is 1.2.4.3. or 2.1.4.3. depending on the size of the animal. The dorsal arms undergo a number of drastic changes. The larvae can be divided, for convenience, into several stages, based in part on the development of the dorsal arms and their web.

Stage I (ML 5.0–8.0 mm, Fig. 2, a, b).—Arms I are largest with suckers of normal size. The arm tips of I and II are spatulate with the suckers on that area replaced by two rows of elongate papillae.

The web is rudimentary. The "kolliker stage" of Naef (1923) corresponds to this stage. Pores are absent or just beginning to open to the outside. The mantle and head are wide (Fig. 13), with indices as high as 100. The funnel organ (Fig. 5a) is W-shaped. The anterior edge of the mantle is demarcated from the head along its dorsal surface by a lighter coloration and by muscular mantle tissue (Fig. 2a).

The dorsum of the mantle is sparcely covered with light brown chromatophores. The head bears two large, dark reddish-brown chromatophores adjacent to the median axis. Five smaller cromatophores are located near the eyes. Two rows of chromatophores are found on the aboral surface of the arms; they may be in a single row basally. The periphery of the eyes is heavily invested with chromatophores. The ventral surface of the mantle and head is much lighter, with only a few scattered chromatophores present.

Stage II (ML 8.0–13.0 mm, Fig. 2, c, d).—Arms II are nearly as long as arms I. The tips of II are still spatulate, with two rows of elongate papillae. The arm tips are slender, with uniserial suckers near the extremities. There are no papillae. Relative growth of the suckers on arms I and II has decreased so that a slight differentiation of the suckers is seen. The web between arms I and II is prominent and subequal in depth. Water pores are visible, especially on the dorsal surface of the head. The mantle and head are narrower and more closely resemble the adult shape. The junction of the head and mantle is still visible. The eyes are directed laterally. The funnel organ is W-shaped. In larger females of this stage, several folds of tissue appear on the funnel organ (Fig. 5b). The chromatophore pattern is essentially the same as that described for the previous stage but the chromatophores on the dorsal surface of the head are less distinct.

Stage III (ML 13.0–15.0 mm).—Arms I are longest with the web extending to the arm tip as a bordering membrane distally. A long round filament extends from the tip of the arm (Fig. 2, c, d). Embedded in the membrane are a number of spherical bodies, located in one row along each side of the arm (Fig. 5e). These (Fig. 5d) consist of glandular epithelial cells which form the web pouches of the adult.

On arms I, the first two or three suckers are uniserial, becoming biserial for about 4/5 of the length of the arm. Near the arm tip the suckers again become uniserial and continue to the base of the filament, which lacks suckers (Fig. 5e). The tips of arms II are the same as in stage II.

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Figure 3. *T. violaceus violaceus*, females. a–b. ML 16.2 mm; a, dorsal view; b, ventral view; c–d. ML 161.8 mm; c, dorsal view; d, ventral view.

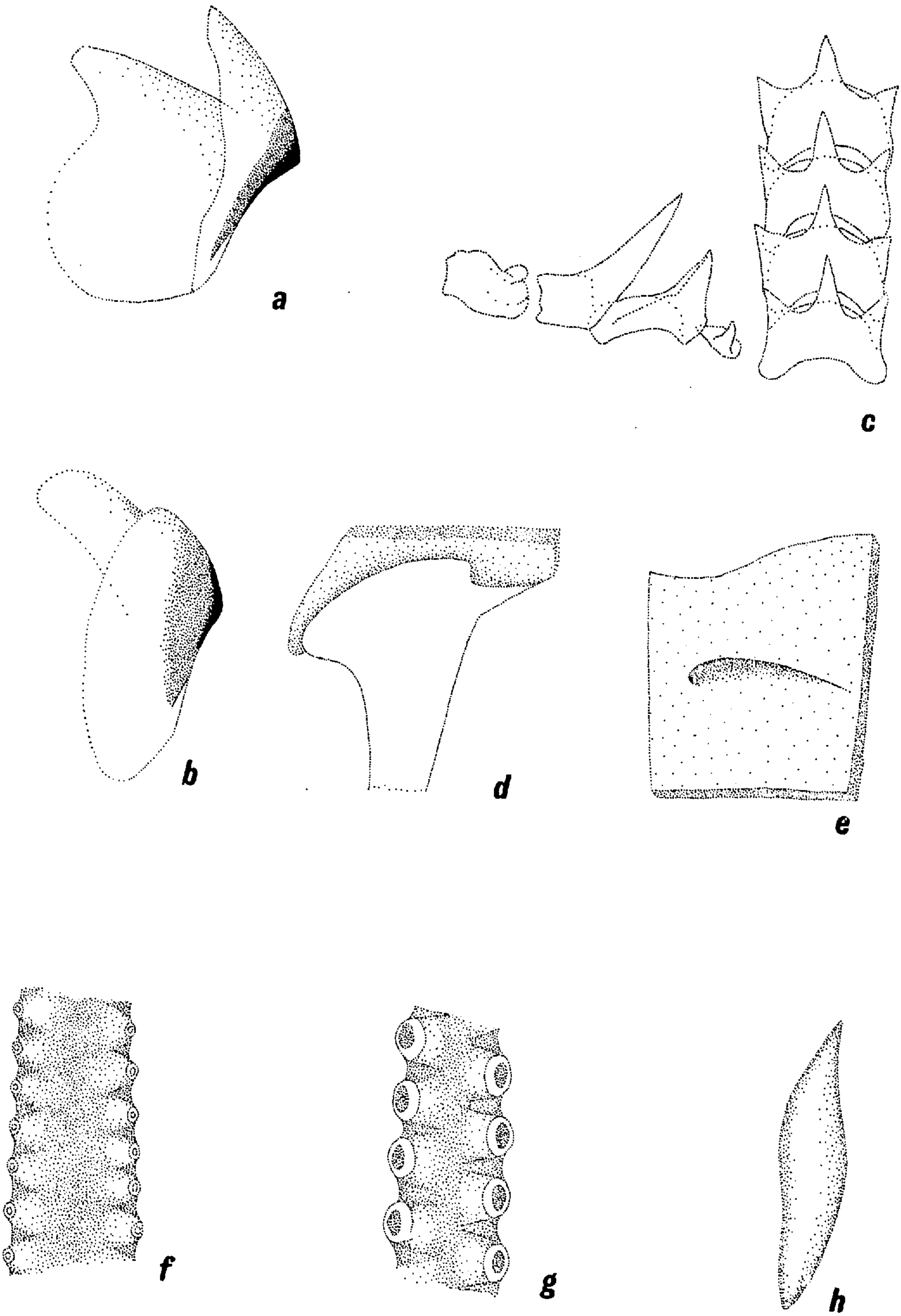


Figure 4. *T. violaceus violaceus*, females. a–b, beaks; c, radula; d–e, funnel and mantle components of funnel-mantle locking apparatus, respectively; f, mid-portion of arm II; g, mid-portion of arm IV; h, dorsal stylet.

The web is well-developed and the water pores are fully open. The mantle and head have decreased in relative width and the eyes are proportionately smaller (Fig. 13).

The chromatophores, especially on the dorsal surface of the mantle and head, are more numerous and obscure the junction of the head and mantle. Chromatophores are also numerous on the arms. The animals show a distinct reddish-brown coloration.

Stage IV (ML 15.0–25.0 mm, Fig. 3, a, b).—The distal filaments of arms I are broken off in advanced females of this stage and the remaining portions of the arms are nearly equal in length. An expanded thick and darkly pigmented membrane surrounds the end of the arm. It bears spherical bodies along its edge, located about 4.8 mm from the margin of the arm. Web sector B joins with this membrane. The suckers are reduced in size on these arms, especially on arms II, where they are found at the edges of the flattened oral surface. The papillae at the tips of the arms are less prominent. Web sector A is also slightly truncated medially, having the characteristic cleft. Arms II are the longest. The mantle and head continue to decrease in relative width (Fig. 13). The W-shaped funnel organ is obscured by an increasing number of tissue folds on its surface.

The aboral surface of the arms contains numerous small chromatophores. The dorsal surface of the head is darkened due to the large number of small, closely spaced chromatophores. The junction of the mantle and head is no longer clear. The ventral surface of the mantle shows the incipient iridescence found in larger animals.

Stage V (ML 25.0–80.0 mm).—Animals in this stage are juveniles. The females have nearly attained the adult proportions, but are not yet sexually mature. The typical adult coloration pattern is present.

Stage VI (ML 80.0–300.00 mm. Figs. 1, a, b, 3, c, d).—This final stage is represented by sexually mature females.

Description of the Males

Adults.—Males (Fig. 6, c, d) attain a mantle length of only about 15 mm (Voss and Williamson, 1971), thus showing a high degree of sexual dimorphism in terms of size with the females. In many respects the adult males resemble larval females.

The males do not have the striking coloration of adult females. In alcohol-preserved males, the dorsal surface of the mantle and head is covered by a moderate number of small chromatophores. Two to three rows of chromatophores extend along the aboral surface of the arms. The chromatophores are set further apart on the ventral surface of the mantle and head.

The mantle is smooth, bowl-shaped and broad posteriorly. The head is slightly wider than the mantle and separated laterally from it by a prominent constriction. The dorsal surface of the head is continuous with that of the mantle. The eyes are large and directed laterally.

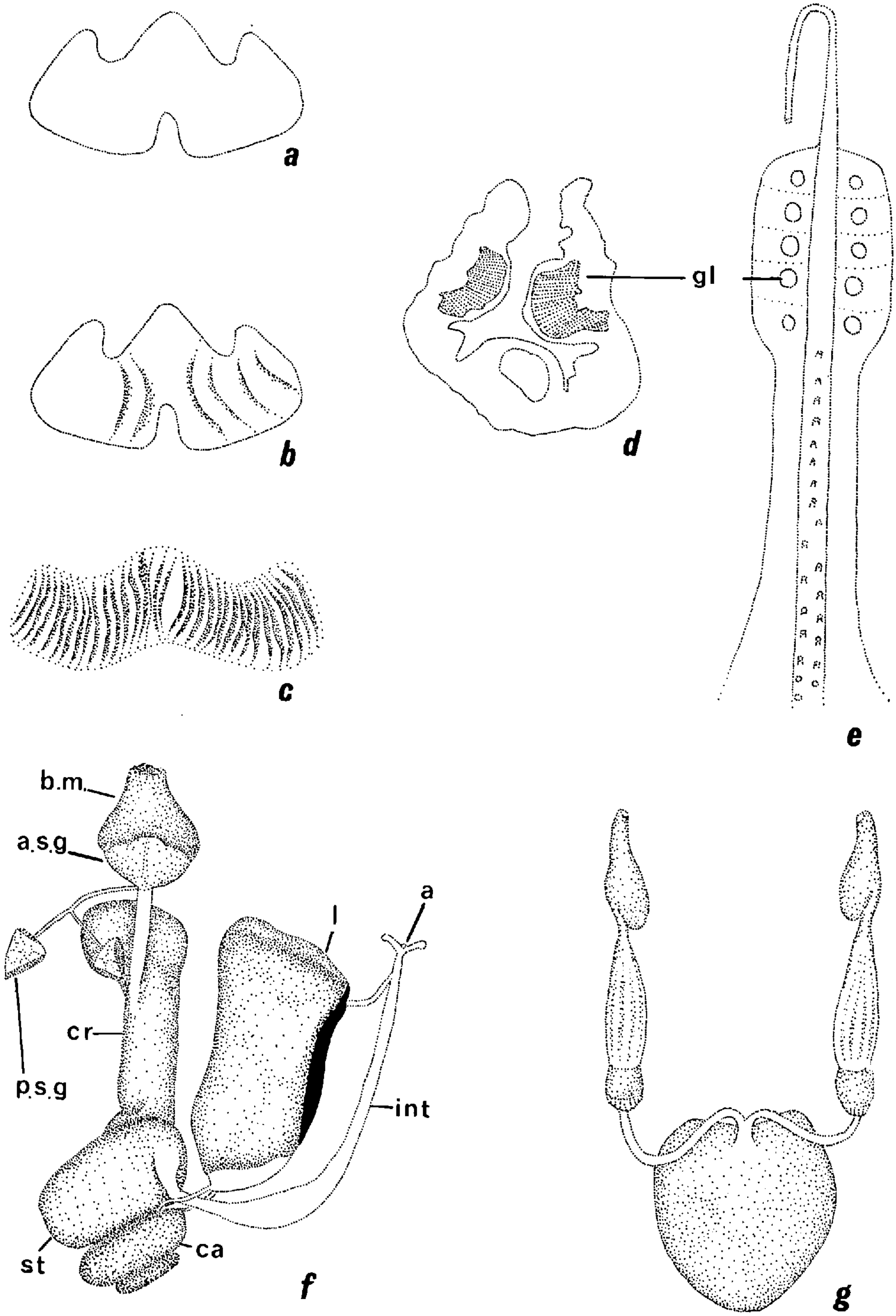
Cephalic water pores are present. As a result of the presence of the large hectocotylus, coiled up in its pouch, the right ventral pore is crowded and degenerate.

Dorsal stylets are embedded in the mantle wall at the insertion of the funnel retractor muscle. They are straight, slender rods measuring 0.56 × 2.56 mm.

The arm order is 2.1.4.3. or 1.2.4.3. Arms I are intact and unmodified in the adults. The suckers are biserial, narrow at the apex and wider at the base. On all the arms (except the hectocotylized arm) the suckers gradually decrease in size toward the arm tips. There are no modified suckers.

The web formula is B.A.E.D.C. or A.B.E.D.C. with sectors A and B the deepest. The web is thin, of uniform structure, and without epithelial modifications (such as pouches). There is no deep cleft in sector A. Sectors A and B are subequal. There are no spherical bodies or thread-like filaments.

The funnel extends beyond the eyes and is free for about ⅓–¼ of its length. The funnel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organ is W-shaped with about 15–20 longitudinal folds which are not as extensive as in adult females.

The digestive system does not differ significantly from that of the female. The buccal mass is small and contains the anterior salivary glands. The posterior salivary glands are large, nearly half the size of the buccal mass. A short, slender esophagus leads from the buccal mass to a small crop. The crop narrows before merging with the muscular stomach. Closely attached to the stomach is the spiral caecum which is connected with the liver by two ducts. The intestine passes between these ducts and terminates in the anus, which bears two anal flaps.

The large, dark brown liver is the most conspicuous feature of the digestive tract. The pancreas is revealed by a light area on its posterior surface. The flask-shaped ink sac is embedded in the dorsal surface of the liver.

With the large number of males available for study, the male reproductive system can be described for the first time. The reproductive tract (Fig. 7, a, e) differs markedly from that of *Octopus*. The sperm are formed in a large testis. From it, they pass through a long, slender *vas deferens* which enlarges as the first accessory spermatophore gland. In this gland, the encapsulation of the single, large spermatophore begins. Additional coatings are produced in a coiled diverticulum, the second accessory spermatophore gland, which leads to a small blind sac (Fig. 7a). This sac then enlarges greatly and contains the coiled, ripe spermatophore whose sperm mass ruptures and fills the sac (Fig. 7e). This blind sac corresponds to Needham's sac of *Octopus* in which a duct leading from Needham's sac to a penis lying in the mantle cavity is responsible for the transfer of spermatophores to the hectocotylized arm.

There is no penis in *Tremoctopus*. Needham's sac is a blind sac and the entire sac with the enclosed spermatophore apparently is transferred directly to the tip of the hectocotylized arm which forms a chamber for its retention. The details of this transfer and how it is accomplished are still unknown. Apparently only a single spermatophore is produced in the lifetime of the male.

In the tissue surrounding the viscera of young males, an area near the base of the left gill is very thin (Fig. 7f) and conspicuous from the absence of chromatophores. The developing Needham's sac lies directly under this region. Apparently removal of the sac and the ripe spermatophore by the hectocotylized arm occurs through rupture at this point.

The hectocotylized arm developes in a pouch between the second and fourth right arms. As the arm increases in size, this large pouch gives the animal a conspicuously asymmetrical appearance. According to Naef (1923), the arm breaks free of the pouch at maturity through an opening at the base of the pouch.

The hectocotylized arm (Fig. 8a) has unusual modifications compared to the hectocotylus of *Octopus*. The arm is constricted at its base and there is a single sucker at this constriction. The proximal half of the arm contains about 22–23 rows of biserially arranged suckers, circular in cross section. A fringed area consisting of closely spaced filaments lies lateral to each sucker pair. These filaments are arranged in rows with 4–5 filaments per row.

The distal portion of the arm (Fig. 8a) bears 15–19 pairs of suckers which are not

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Figure 5. *T. violaceus violaceus*, females. a–c. funnel organs; a, ML 7.0 mm; b, ML 12.4 mm; c, ML 161.8 mm; d, section through dorsal arm of young female (e) showing glandular bodies; e, dorsal arm of young females, ML 16.8 mm; f, digestive tract; g, reproductive tract. Explanation of abbreviations: a, anus; a.s.g., anterior salivary gland; b.m., buccal mass; ca, caecum; cr, crop; gl, glandular tissue; i, ink sac; int, intestine; p.s.g., posterior salivary gland; st, stomach.

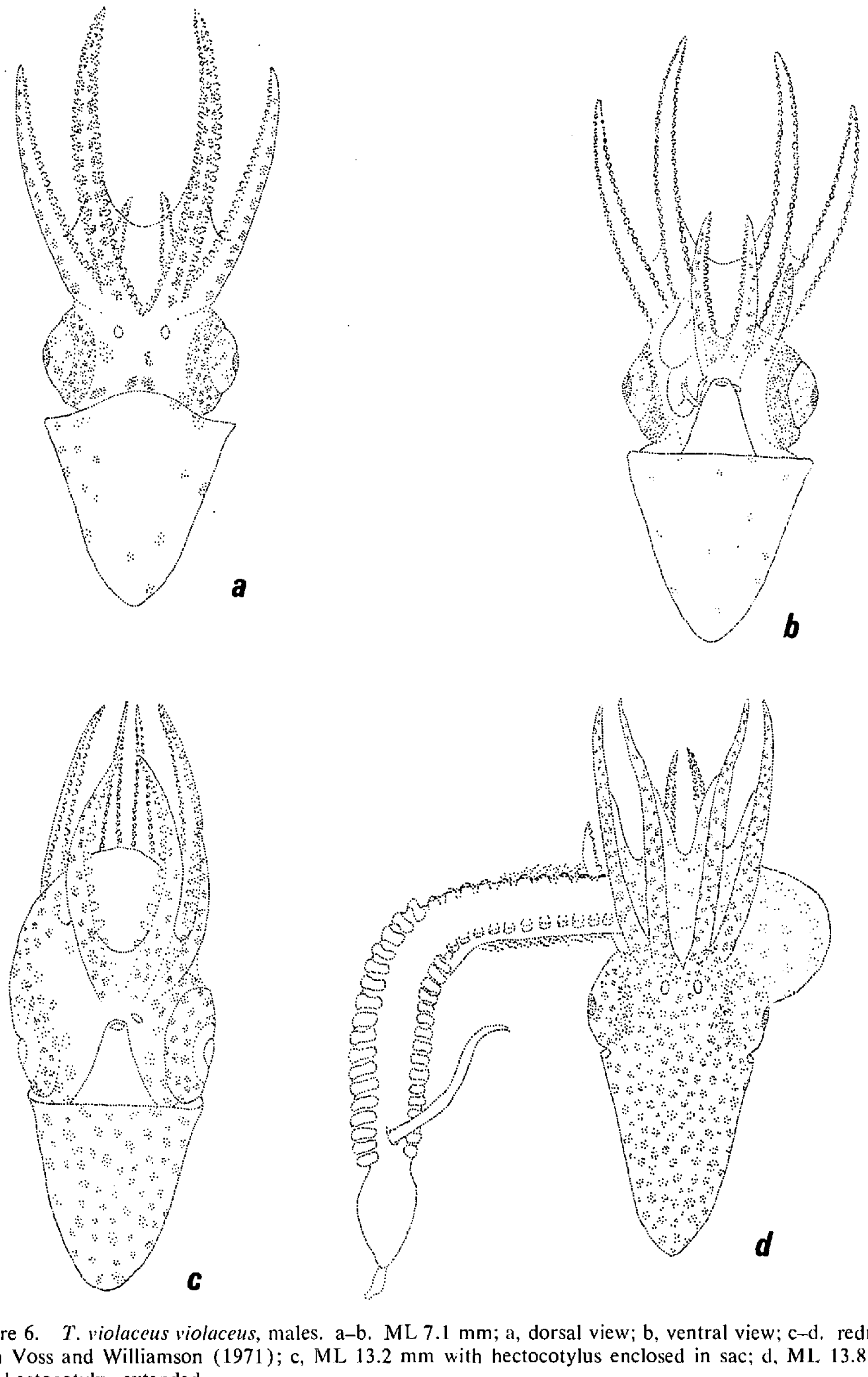


Figure 6. *T. violaceus violaceus*, males. a–b. ML 7.1 mm; a, dorsal view; b, ventral view; c–d. redrawn from Voss and Williamson (1971); c, ML 13.2 mm with hectocotylus enclosed in sac; d, ML 13.8 mm with hectocotylus extended.

bordered by the fringe of filaments. The two most proximal pairs are circular in shape and the remaining pairs are transversely flattened. A long filament (the "penis" of Naef) extends from between the second and third distal pairs of suckers.

The distal tip of the arm has a swollen sac, the spermatophore reservoir, which serves as a place of storage for the spermatophore (Fig. 8, d, e). This reservoir connects with the penial filament by means of a duct that passes into the filament.

In a mature hectocotylized arm, the sperm reservoir is a swollen sac within which is a mass of coiled, pinkish, thread-like tubules. The spermatophore passes into the duct connecting the reservoir with the penial filament (Fig. 8e).

Tremoctopus autotomizes its hectocotylized arm during mating (Robson, 1932). Sexually mature females are frequently found with these detached arms (often more than one arm per female) lying in the mantle cavity. The autotomized arm typically lacks the "penis," and the spermatophore reservoir at the tip of the arm has usually burst.

There are no published descriptions of the spermatophore of *Tremoctopus*. The spermatophore is very long and slender (Fig. 8f). In a mature animal, it does not contain the intact sperm mass; only the portion from the cement body to the oral cap is present (Fig. 9). The cement body is smooth and narrows at its anterior end. The horn is smooth from the cement body to its midportion where it makes three turns, then narrows, and continues to the cap as a scaled structure. In the specimen examined, the cap did not contain an ejaculatory thread.

Juveniles (Fig. 6, a, b).—In mature animals, the mantle length is only about 14–15 mm. Developmental changes, consequently, are not as striking as those seen in the females.

The mantle is very wide and bowl-shaped (Fig. 17). During growth, the relative width of the mantle becomes narrower. Similarly, the relative width of the head decreases with growth and the eyes become less prominent.

In proportionate size, the arms grow isometrically. The web is rudimentary in newly hatched animals and increases in depth, particularly in sectors A and B.

The funnel is W-shaped. During growth, the number of folds on the organ increases to a maximum of 15–20.

The number of gill lamellae in the outer demibranch (9–11) does not change during growth.

The hectocotylus develops in an enclosed sac between the second and fourth right arms.

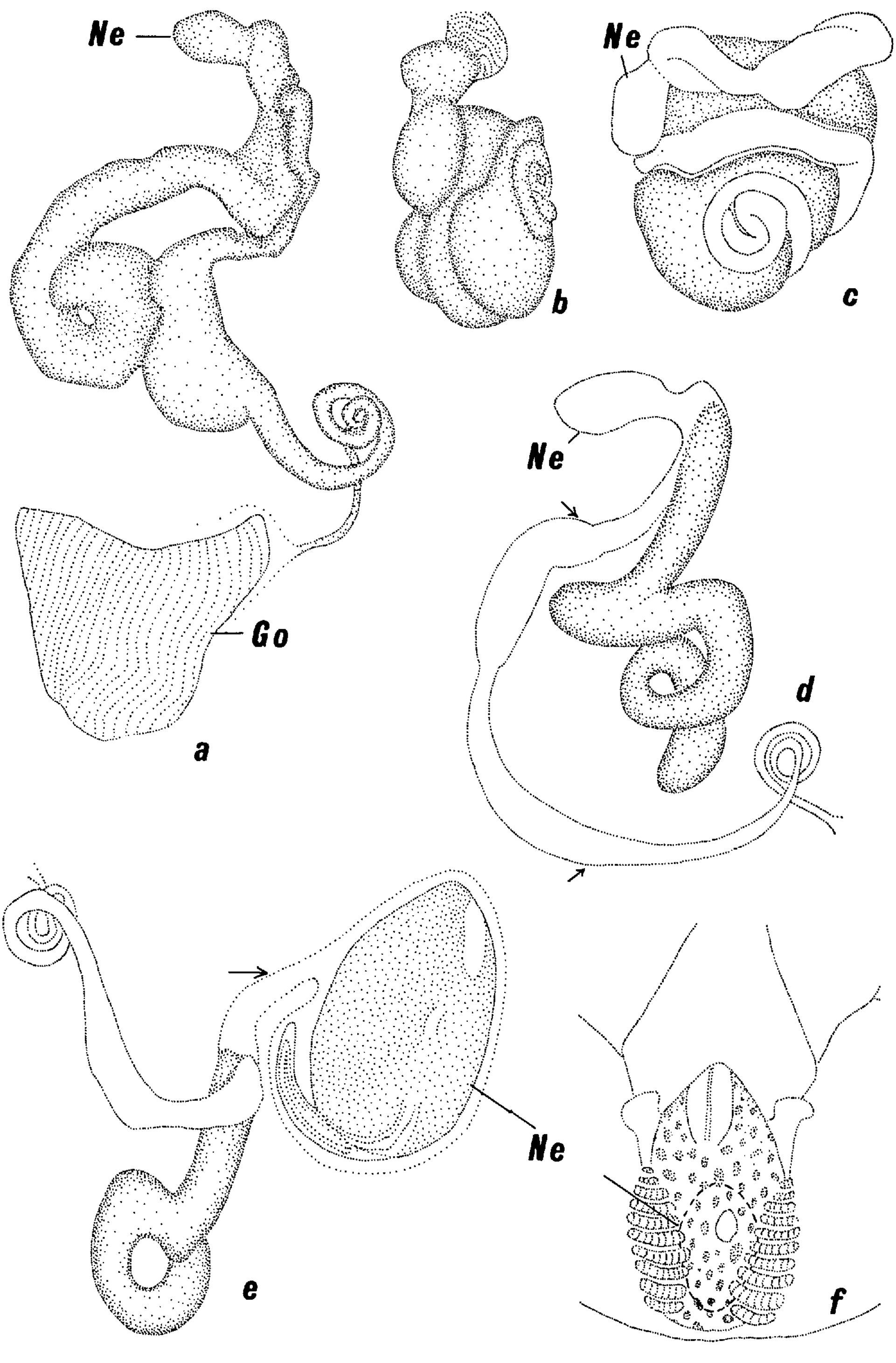
Initially, the hectocotylus is a long, slender structure with a single row of suckers (Naef, 1923). Later, the suckers become biserially arranged. In the course of its development, the spermatophore reservoir is moved from a position proximal to the distally located penial filament to a position at the tip of the arm with the penis proximal to the reservoir (Fig. 7, b, d). The hectocotylus apparently breaks free of the enclosing pouch through a pore in the sac.

The uncoiled hectocotylized arm was 11.6 mm long in a specimen with a mantle length of 9.8 mm. The proximal half of the arm had biserial suckers, with circular aperatures. These were bordered by the papillae which at this stage of development were very short, rudimentary projections from the arm. The distal half of the arm contained the biserial transverse suckers found in the adults. The penial filament was long (about 9.8 mm) and opened between the second and third pairs of suckers. At the arm tip, the spermatophore reservoir was already formed, but was present only as a deflated sac (Fig. 8c), rather than being distended with the sperm mass. At a mantle length of about 11–12 mm, the hectocotylus (still enclosed within its sac) has the characteristic features found in the adult.

Type.—Could not be located.

Type Locality.—Mediterranean Sea.

Distribution.—Gulf of Mexico, Caribbean Sea, Atlantic Ocean, Mediterranean Sea, between latitudes 40°N and 35°S.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Tremoctopus violaceus gracilis (Eydoux and Souleyet, 1852)

Octopus gracilis Eydoux and Souleyet, 1852: 13.

?*Octopus dubius* Eydoux and Souleyet, 1852: 13.

Tremoctopus gracilis, Tryon, 1879: 131.—Hoyle, 1886a: 71.—Robson, 1932: 214, Nesis, 1971: 514.

?*Tremoctopus dubius*, Tryon, 1879: 131.—Hoyle, 1886b: 215.

Tremoctopus quoyanus, Hoyle, 1886a: 70 (pars): 1886b: 214 (pars): 1904: 12, 1909: 258.

Tremoctopus violaceus Wulker, 1910: 5.—Berry, 1912: 281.—Wulker, 1920: 51.—Sasaki, 1929: 29.—Robson, 1932: 206 (pars).—Adam, 1942: 17.—Benham, 1944: 294.—Dell, 1952: 71.—Akimushkin, 1955: 368.—Jones, 1963: 764.—Voss, 1967: 86 (pars).—Rancurel, 1970: 70.—Voss and Williamson, 1971: 110.

Tremoctopus lucifer Akimushkin, 1963: 152.

Material Examined.—33 males and 70 females from the following stations and locations: 1♂, ML 13.3 mm, Pinta Bank, Galapagos, F. Alverson, 12 August 1957, surface, UMML 31.1099.—1♀, ML 6.2 mm, 6♂♂, ML 4.9–6.2 mm, Messina (Mediterranean), Oslo Museum.—1♀, ML 16.0 mm, Natal IKMT No. 46, 26°42′S, 40°07′E, 22 February 1962, in 500 m, SAM A29751.—1♀, ML 54.0 mm, HUGH M. SMITH, Cr. 30, Sta. 99, 38°07′N, 57°30′W, 22 August 1955, surface, USNM.—1♀, ML 22.2 mm, HUGH M. SMITH, Cr. 38, Sta. 29, 08°27.5′S, 130°02.7′W, 12 February 1957, surface, USNM.—1♂, ML 10.9 mm, ALBATROSS Sta. 3929, 23°19′N, 166°54′W, 13 May 1902, surface, CASIZ.—1♀, ML 15.8 mm, ALBATROSS Sta. 3930, 25°07′N, 170°50′W, 15 May 1902, surface, CASIZ.—1♀, ML 9.8 mm, 1♂, ML 9.3 mm, ALBATROSS Sta. 3878, 14 April 1902, CASIZ.—2♀♀, ML 13.8–15.8 mm, SOYO-MARU Sta. 5, 30°N, 138°51.5′E, 18 November 1972, surface TRFRL.—1♀, ML 16.3 mm, SOYO-MARU Sta. B2, 34°04.5′N, 139°59.5′E, 20 June 1972, surface, TRFRL.—2♀♀, ML 16.9–18.8 mm, SOYO-MARU Sta. K18, 35°47.3′N, 144°00.8′E, 5 July 1971, surface, TRFRL.—6♀♀, ML 12.8–38.6 mm, 2♂♂, ML 10.1–10.8 mm, 29°N, 135°E, June/August 1969, surface, TRFRL.—2♀♀, ML 13.3–73.1 mm, SOYO-MARU Sta. 16, 32°28.3′N, 138°51.5′E, 3 August 1971, surface, TRFRL.—2♀♀, ML 59.9–74.9 mm, SOYO-MARU Sta. 56, 30°50.6′N, 142°30.2′E, 22 June 1972, surface, TRFRL.—2♀♀, ML 8.8–13.0 mm, 1♂, ML 10.1 mm, HORIZON, Cr. Shellback, Sta. 50, 01°27′N, 109°40′W, 7 June 1952, surface, S10.—4♀♀, ML 11.0–12.2 mm, ARGO, Cr. Monsoon, Sta. 6, 14°56′S, 152°53′E, 5 October, 1960, surface, S10.—1♀, ML 10.9 mm, ARGO, Cr. Lusiad, Sta. 30, 29°51′S, 11°07′W, 12 June 1963, surface, S10.—2♀♀, ML 9.8–11.4 mm, HORIZON, Cr. Shellback, Sta. 83, 00°53′N, 97°11′W, 24 June 1952, surface, S10.—2♀♀, ML 13.4–17.8 mm, ARGO, Cr. Monsoon, Sta. 1, 20°12′N, 134°52′W, 30 August 1960, surface, S10.—3♀♀, ML 11.1–14.9 mm, 1♂, ML 11.0 mm, THOMAS WASHINGTON, Cr. Seven Tow, Sta. 159, 30°20′N, 156°15′W, surface, S10.—1♀, ML 7.0 mm, 7♂♂, ML 3.9–11.6 mm, HORIZON, Cr. Shellback, Sta. 51, 02°16′N, 109°12′W, 8 June 1951, surface, S10.—3♀♀, ML 15.9–22.6 mm, SPENCER F. BAIRD, Cr. Tethys, Sta. 38, 26°14′N, 141°35′W, 9 July 1960, surface, S10.—1♀, ML 16.9 mm, HORIZON, Cr. Shellback, Sta. 81, 02°42′N, 97°27′W, 23 June 1952, surface, S10.—5♀♀, ML 8.1–11.8 mm, ARGO, Cr. Climax 11, Sta. E7, 05°04′N, 155°00′W, 24 September 1969, surface, S10.—2♀♀, ML 14.6–15.9 mm, HORIZON, Cr. Shellback, Sta. 44, 5 June 1952, surface, S10.—2♀♀, ML 10.0–11.5 mm, 1♂, ML 9.3 mm, ALEXANDER AGASSIZ, Cr. 6608G, Sta. 120, 25°13′N, 120°23′W, 8 August 1966, surface, S10.—1♀, ML 10.8 mm, 1♂, ML 14.0 mm, ANTON BRUUN, Cr. MV 65-IV, 33°31′S, 75°18′W, 17 July 1965, surface, S10.—2♀♀, ML 7.7–13.1 mm, 1♂, ML 5.9 mm, HORIZON, Cr. Capricorn, Sta. 159, 15°39′S, 114°14′W, 4 February 1953, S10.—3♀♀, ML 33.8–40.4 mm, STRANGER, Cr. Naga, Sta. 59-004, 23°20′N, 139°03′W, 22 June 1959, surface, S10.—8♀♀, ML 11.7–24.7 mm, 1♂, ML 15.5 mm, SPENCER F. BAIRD, Cr. Tethys, Sta. 29, 27°05′N, 136°25′W, 10–11 August 1960, surface, S10.—1♂, ML 7.6 mm, HORIZON, Cr. Shellback, Sta. 48, 00°08′S, 110°40′W, 7 June 1952, surface, S10.—1♂, ML 11.0 mm, ALEXANDER AGASSIZ, Cr. Ursa Major 11, Sta. 33, 35°35′N, 154°59′W, 8 September 1964, surface, S10.—1♂, ML 10.6 mm, 06°40′S, 115°03′W, 4 June 1952, surface, S10.—2♀♀, ML 7.5–7.9 mm, ARGO, Cr. Climax 11, Sta. E9, 01°N, 155°W, 26 September 1969, surface, S10.— 1♂, ML 10.7 mm, HORIZON, Cr. Downwind, Sta. 24, 34°31′S, 79°30′W, 20 August 1957, S10.—1♂, ML 13.8 mm, HORIZON, Cr. Downwind, Sta. 29, 22°38′S, 72°00′W, 2 January 1958, surface, S10.—1♂, ML 8.8 mm, HORIZON, Cr. Downwind, Sta. 38, 21°10′S, 113°46′W, 9 February 1958, surface, S10.—1♀, ML 7.9 mm, 3♂♂, ML 11.1–13.2 mm, HORIZON, Cr. Downwind, Sta. 31, 22°27′S, 78°26′W, 9 January 1958, surface, S10.—1♂, ML 37.8

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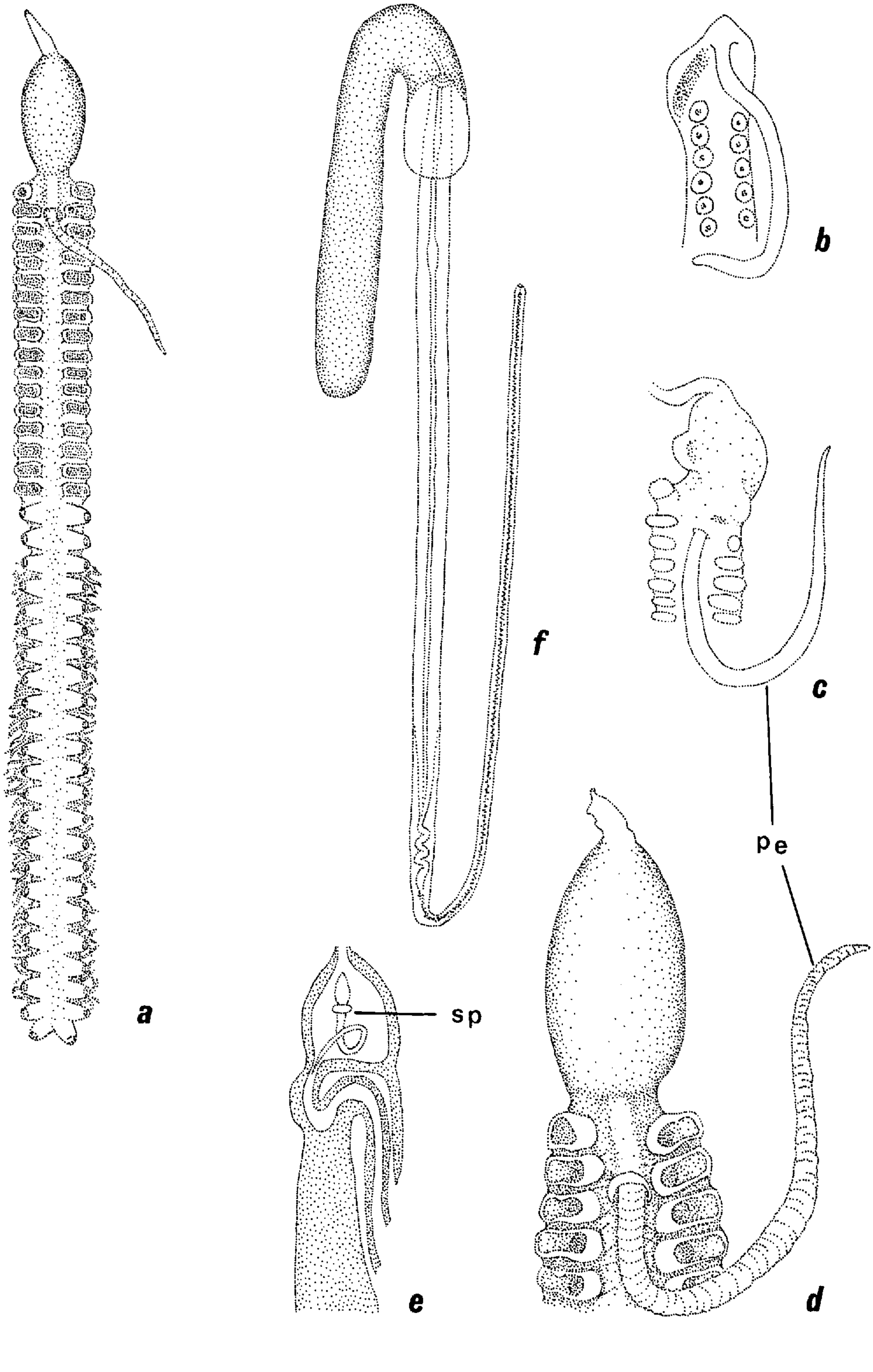
Figure 7. *T. violaceus violaceus*, males. a, immature animal with sperm still in gonad; b–d. Nearly mature male with sperm in accessory spermatophore gland; b, *in situ* dissection; c, same, with reproductive organs rotated 90° counterclockwise; d, same, with organs uncoiled. The arrows indicate the area occupied by the developing spermatophore; e, male with encapsulated, ripe spermatophore lying in the distended Needham's sac. The arrow indicates the point of rupture during removal of the sac; f, male with mantle pinned back to expose viscera. Hole in tissue surrounding viscera indicates point of spermatophore removal. Go, gonad; Ne, Needham's sac.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mm, SOYO-MARU, Sta. 24, 31°35.7'S, 96°17'W, 26 January 1963, from stomach of *Alepisaurus*, UMML.

Diagnosis.—Mantle firm, muscular; coloration of adult females bluish purple on dorsum and silvery gold on ventrum; distal portion of hectocotylus with 19–22 pairs of suckers and proximal portion with 27–29 pairs.

Description.—This species is very similar to *T. violaceus violaceus*. Variations in morphometry between the two subspecies are given in Tables 10 and 11. *T. v. gracilis* is so similar to *T. v. violaceus* that the description of the males and females of one serves equally well for the other except in the details of the hectocotylus and the differences in gill lamellae. Therefore there is no useful purpose in giving a full description of the subspecies.

The most striking difference between these two subspecies is the number of suckers on the hectocotylized arm of the males. The distal portion of the arm in *T. violaceus gracilis* has 19–22 pairs of transverse suckers, while in *T. violaceus violaceus* there are only 15–19 pairs. In *T. violaceus garcilis* there are 27–29 pairs of suckers on the proximal portion of the arm while there are 22–23 pairs in *T. violaceus violaceus*.

Although the gill filament counts have the same range of values in the two subspecies (13–16), the mean is higher in *T. violaceus gracilis* (*T. violaceus violaceus* 13–*13*–16; *T. violaceus gracilis* 13–*15*–16).

Type.—Not found (Paris?).

Type-Locality.—106°W, 08°N (Pacific Ocean).

Distribution.—This species occurs in the Pacific and Indian oceans, between latitudes 39°N and 30°S.

Tremoctopus gelatus new species
Figures 10–12

Tremoctopus violaceus, Voss, 1967: 86 (pars).

Material Examined.—HOLOTYPE: a ♀, ML 328 mm, Boynton Municipal Beach, Boynton, Florida, collected by T. Lovins, 20 May 1971, beach stranding, USNM 727076. PARATYPES: 1 ♀, ML 225 mm, Boynton Municipal Beach, Boynton, Florida, T. Lovins, 14 April 1971, beach stranding, UMML 31.1108.—1 ♀, ML?, Crandon Park Beach, Key Biscayne, Florida, Mrs. Joan Gill, March 1964, UMML.—2 ♀ ♀, ML 26.0–40.0 mm, JOHN R. MANNING Cr. 26, Sta. 6, 36°11'N, 149°00'W, 22 July 1955, USNM 727077.—1 ♀, ML 24.0 mm, 31°44'S, 44°35'E, 15 August 1962, 500 m, from stomach of *Alepisaurus ferox*, SAM A29712.—1 ♂, ML 10.0 mm, ALEXANDER AGASSIZ, Cr. Ursa Major, Sta. 36, 31°29'N, 155°00'W, 10 September 1964, surface, S10.

Diagnosis.—Tissue of mantle, head and arms gelatinous, transparent; eyes very large; water pores reduced in size; 8–11 gill filaments on outer demibranch in females, 7–8 in males.

Description of the Females

Adults.—(Fig. 10, a, b). The living animal is pale orange-red over the entire surface with minute widely diffused chromotophores but is transparent as to permit reading of newsprint through the tissue (G. Voss, personal communication). In the preserved state the mantle is reddish-brown dorsally and nearly colorless ventrally.

The mantle is wide and tapers to a broad posterior point. Its wall is thick as in *T. violaceus*, but is gelatinous. The surface is smooth.

The head is slightly narrower than the mantle. Its tissue is also gelatinous. The eyes are much larger than in *T. violaceus*. The cephalic pores are small ($PLI_d = 2–4$).

The arms are long, stout, gelatinous, and in the order 2.4.3.1. (Table 1). The distal portions of arms I are lost. The suckers on

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Figure 8. *T. violaceus violaceus*, males. a, mature hectocotylized arm; b, tip of arm of very young male (from Naef, 1923); c, same of nearly mature male; d, same from mature male shown in (a); e, cross section of same to show internal structure (from Naef, 1923); f, spermatophore. Explanation of abbreviations (abbreviations apply to 5d and 5e also): pe, penial filament; sp, spermatophore.

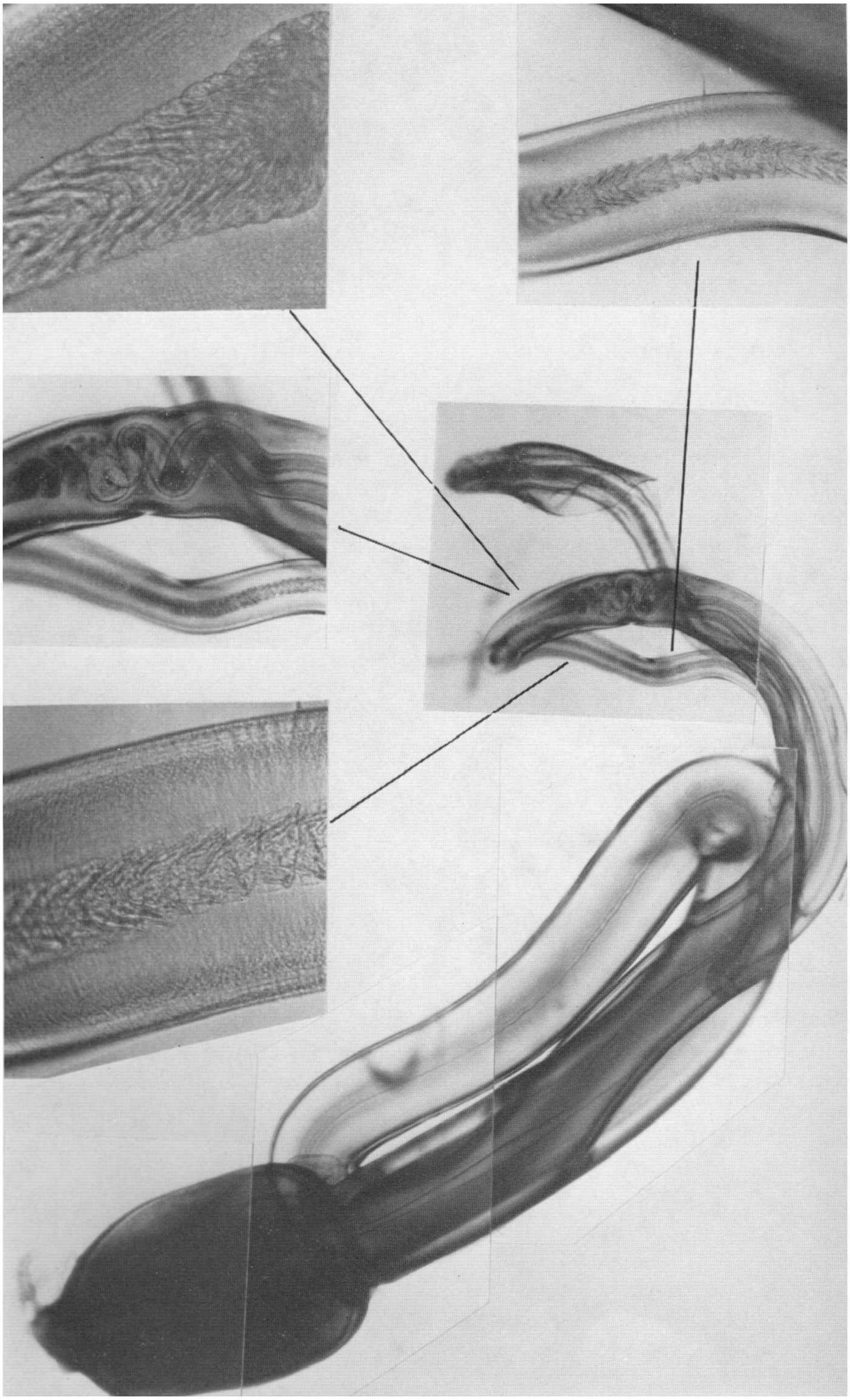


Figure 9. *T. violaceus violaceus*, spermatophore.

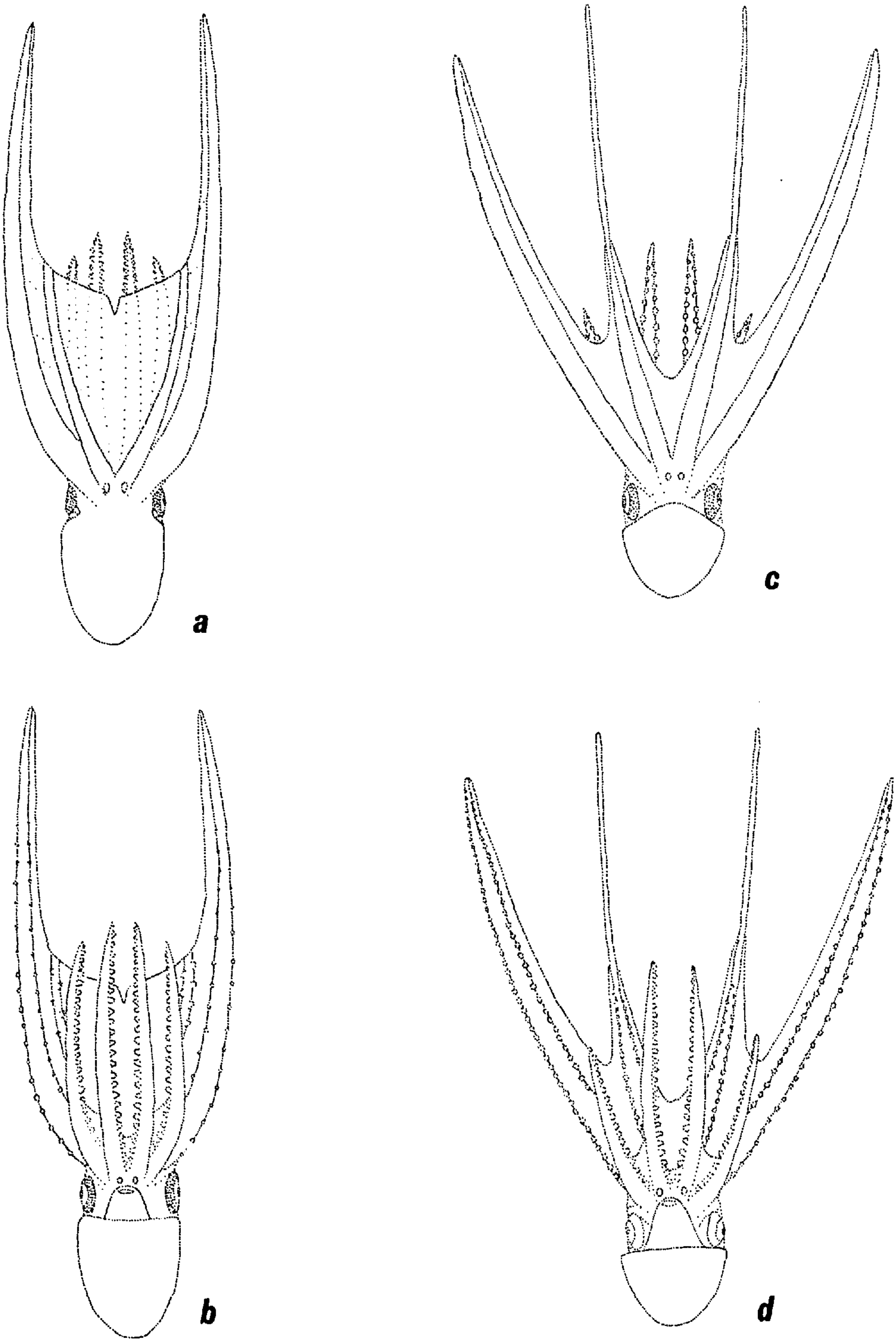


Figure 10. *T. gelatus*, females. a–b. ML 328.0 mm; a, dorsal view; b, ventral view; c–d. ML 26.0 mm; c, dorsal view; d, ventral view.

Table 1. Measurements (in mm) and indices of four females and one male of *Tremoctopus gelatus*, new species

		Holotype		Atlantic		Pacific		Indian			
ML		328		225		25.0		20.7		10.0	
MW		221		157		27.9		11.9		11.2	
HW		205		139		22.0		15.9		10.0	
AL	I	L	R	L	R	L	R	L	R	L	R
	I	441+	366+	----	328+	116.1	98.2	83.4	74.4+	13.0	16.0
	II	818+	1,106	----	----	93.0	111.5	75.0	69.0	13.9	13.2
	III	560	615	----	408	55.1	58.2	35.8	----	7.0	----
	IV	669	650	----	----	71.0	88.0	49.3	55.2	7.3	7.1
AW	I	29		24		4.1		3.4		1.3	
	II	49		32		5.9		4.0			
	III	37		29		4.1		2.5			
	IV	33		24		4.5		3.1			
Sn		7.7		7.6		1.9		1.1		0.4	
Pl_d		9.0		8.3		1.8		2.0		0.6	
Pl_v		5.6		6.8		2.9		----		0.2	
Gill Number		11		10		11		9		7(8?)	
MWI		67.4		69.8		111.7		57.5		112.0	
HWI		62.6		61.7		88.2		76.9		100.0	
ALI		71.6		----		82.1		80.2		56.9	
MAI		29.7		----		21.4		24.3		62.4	
SnI		2.4		3.4		7.6		5.3			
PLI_d		2.7		3.7		7.2		2.0			
PLI_v		1.7		3.2		11.6		----			

the proximal area are normal, but become smaller in size, set further apart, and are arranged in a single row distally. The suckers are small, elevated, and set upon a broad gelatinous base, the width of which exceeds that of the sucker aperture. Arms II contain biserially arranged suckers which become degenerate along much of the arm. The oral arm surface is flat, with the sucker rudiments located along the lateral edges. In arms III and IV, the suckers are biserial and gradually decrease in size toward the arm tips.

The web appears to be similar to that of *T. violaceus*. Sectors A and B are extensively developed. Web sector A (between the dorsal arms) is marked by a deep cleft. In sector B, the web extends to the tips of the second arms. Sectors C, D and E are much shallower. Although the web is not intact, its formula appears to be B.A.C.D.E.

The funnel is large and extends beyond the level of the eyes. It is free for about ½ of its length. The funnel articulates with the inner wall of the mantle by a transverse pocket on the mantle wall. The funnel organ consists of numerous folds that overlie a W-shaped base.

The gills contain 8–11 filaments on the outer demibranch.

The rachidian tooth of the radula (Fig. 11c) is tricuspid. There is no seriation. The lateral cusps are smaller and rounder than in *T. violaceus*. The first lateral is small with a single curved cusp. The tooth is not set at an angle to the radular row as is the case in *T. violaceus*. The second lateral is large and has a single conspicuous cusp. The third lateral is spinose. The marginal tooth consists of a flat rectangular plate.

Two small, triangular, posterior salivary glands are attached to the esophagus by very small ducts. The slender esophagus passes from the buccal mass and opens into the anterior portion of a moderately large crop which narrows slightly before opening into a well-developed muscular stomach. The externally striated spiral caecum gives rise to a

slender intestine that passes between the two hepatic ducts. The intestine is slender proximally, but medially becomes convoluted and then dilates into a large sac-like structure. The distal portion is slender and terminates in the anus, which bears the two anal flaps.

The liver forms the major portion of the viscera. The pancreas lies in the posterior region of the liver. Also embedded in the liver is the small, elongate ink sac, somewhat smaller than in *T. violaceus.* The ink sac extends along nearly the entire length of the liver, but covers only about ¼–⅕ of its width. A duct from the ink sac joins the intestine near the anus.

The ovary is circular and flattened (Fig. 11b). A small duct arises from it and divides into two slender proximal oviducts. Each oviduct opens into a muscular, expanded oviducal gland. From the oviducal gland the distal oviduct narrows and then enlarges to terminate at the gonopore.

Juveniles.—(Fig. 10, c, d). Three young females of *Tremoctopus gelatus* were examined (Table 1). They were collected from stomach contents of the fish *Alepisaurus.*

In general appearance, these animals show the features seen in the adult females (gelatinous tissue, enlarged eyes, reduced number of gill filaments) and some of the developmental features described for *T. violaceus.*

The preserved animals are whitish to light tan in color. Chromatophores are sparsely distributed over the mantle, head and arms.

The mantle is thin, gelatinous and wide (MWI: 117.6 in the measurable Pacific Ocean specimen; the Indian Ocean animal is in poor condition, but the MWI appears to be only 57.5). The eyes are prominent, much more so than in *T. violaceus* of comparable size. The head is narrower than the mantle (HWI: < 100).

The funnel organ is W-shaped with overlying folds of tissue; more folds are present on the funnel organ of the larger female. The funnel locking apparatus is as in the adults.

The arms are long and in the order 1.2.4.3. Arms I have biserial suckers along most of the arm, but they become uniserial near the tip, from which extends a long, slender suckerless filament. Glandular bodies were not seen in association with the dorsal arms.

Arms II, wide and with a typically flattened oral surface, are actually the most conspicuous arms although they are not the longest in young females. Their biserially arranged suckers become small, closely set and located along the edges of the arms. Arms III and IV contain normal, biserially arranged suckers.

In the smaller specimen from the Pacific Ocean, the web is intact and has the formula B.A.C.D.E. Web sector A forms a smooth arc and there is no trace of a deep cleft.

Description of the Males

Only one male (Fig. 12) of *T. gelatus* was seen collected at the surface in the Pacific Ocean. The following description is based on this specimen (Table 1).

Chromatophores are small and sparsely distributed over the surface of the body, head and arms. There are no large chromatophores on the dorsal surface of the head.

The mantle is thin, but covered with a thick layer of transparent, gelatinous material. Its surface is smooth, without sculpture and wide (MWI: 112%). The head is wide and the eyes are large. The arms are in the order 1.2.3.4, their suckers are similar to those of males of *T. violaceus.*

The funnel extends to the level of the eyes and is embedded along nearly all of its length in the transparent gelatinous tissue of the head. The funnel organ is W-shaped. The gills contain 7–8 filaments on the outer demibranch.

The hectocotylus is very poorly developed (immature) and is enclosed in a sac between the second and fourth right arms. A detached hectocotylus was recovered from the mantle cavity of one of the adult females (Fig. 11a). The proximal half of the arm is absent, but the spermatophore reservoir is

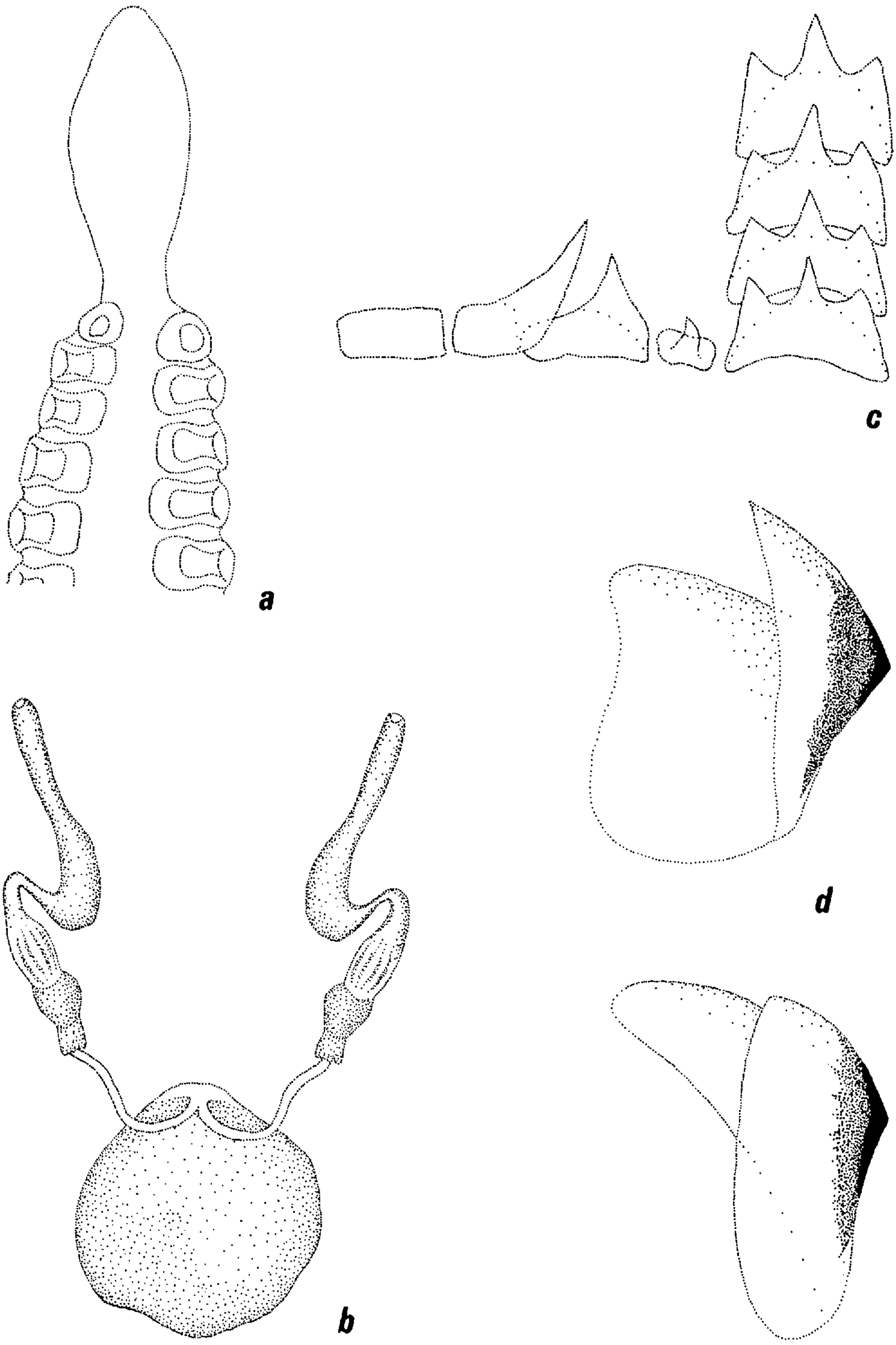


Figure 11. *T. gelatus.* a, tip of hectocotylized arm recovered from adult female; b–d. females; b, reproductive tract; c, radula; d, beaks.

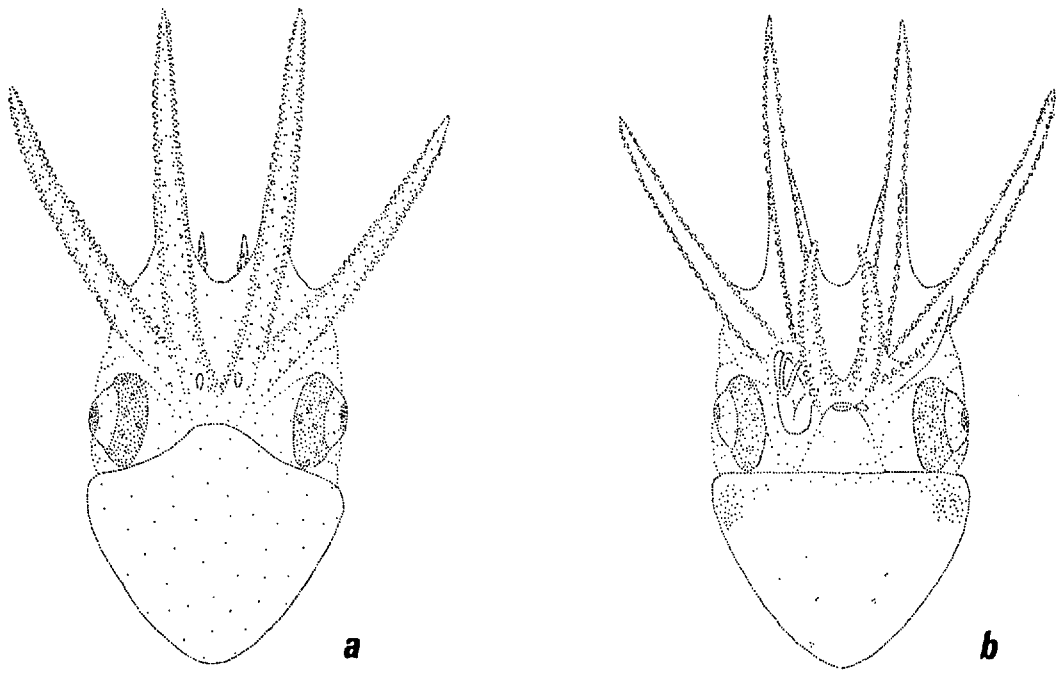


Figure 12. *T. gelatus*, male. ML 10.0 mm. a, dorsal view; b, ventral view.

still intact. A penial filament is not present at the tip of the arm and there is no pore between the distal sucker pairs from which a retracted filament could extend. The suckers are transversely flattened and the lateral portion of the sucker is folded over the aperture, forming a partially closed structure. This all may be an artifact of preservation.

Type.—United States National Museum of Natural History, USNM 727076.

Type-Locality.—Boynton Beach, Florida, U.S.A., (27°N, 85°W), beach stranding.

Discussion.—The development of the females of *T. gelatus* can only be speculated upon since there are so few animals available. *T. gelatus* seems to pass through developmental stages similar to those seen in *T. violaceus* larvae and juveniles. Apparently, however, specimens of *T. gelatus* have the same morphological development as *T. violaceus* at a larger size. This may indicate that, as assumed from adults seen, *gelatus* obtains a larger size than does *violaceus*. This is reinforced by the fact that a female of *T. gelatus* with a mantle length of 20–25 mm parallels the developmental stage of a much smaller female of *T. violaceus* and that the male is at a stage of development seen in much smaller males of *T. violaceus*. The hectocotylus recovered from the mantle cavity of the female, although not complete, suggests it is considerably larger in *T. gelatus* than in *T. violaceus*.

Distribution.—The species is known at present from beach strandings off the eastern coast of Florida, from the waters near the Hawaiian Islands and from the Indian Ocean. It therefore seems to be cosmopolitan in tropical and temperate seas.

Remarks.—This species was first recognized as new by G. Voss from a large female washed ashore alive on Key Biscayne, Florida in March 1964. The mantle contained a hectocotylus that was preserved in the

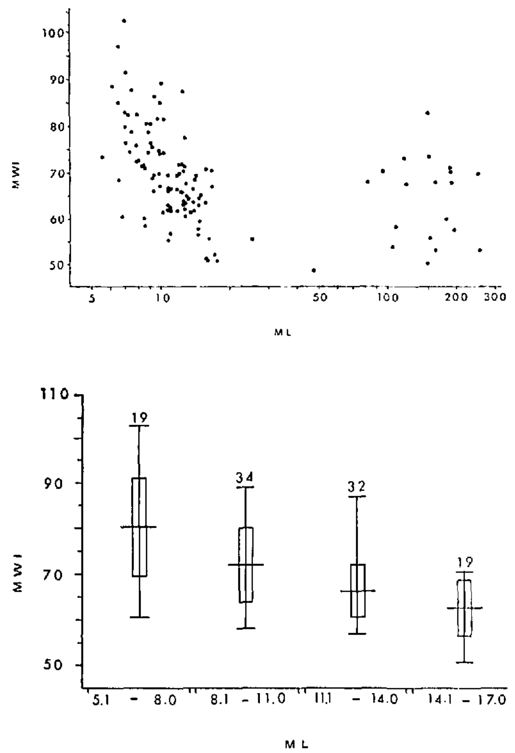


Figure 13. Mantle width index plotted against mantle length in *T. violaceus violaceus* females. All are *T. violaceus violaceus*. (a, values plotted individually; b, animals grouped into size classes.)

research collections of RSMAS. The very large female, in perfect shape, was preserved in formalin, but was eventually accidentally destroyed. No other specimen of this species was seen again on Florida beaches until 1971 when two strandings occurred.

Morphometry

Tremoctopus violaceus violaceus

Many changes occur during the ontogeny of both females and males as seen, for example, in the allometric growth of the mantle, head and arms. Since this species exhibits pronounced sexual dimorphism, the two sexes are treated separately.

The graphs included in this section are of two types: in the first graph of each index, individual measurements are plotted separately while in the second graph the animals are divided into size groups, showing the range and mean ±1 standard deviation for the group.

Females

Mantle Width Index (MWI).—The relative width of the mantle (Fig. 13) decreases with an increase in size of small animals. Later growth of the mantle is isometric. Animals within a particular size group (Fig. 13) show a large amount of variation. Isometric growth of the mantle occurs in adults with a mantle length of 100–250 mm.

Calculations using only the material collected by the Discoverer (Cape Verde Basin) show no significant differences from calculations based also on larvae collected in the Gulf of Mexico and the West Atlantic.

Head Width Index (HWI).—The relative growth of the head is similar to that of the mantle. The change in the head width index is most conspicuous among females less than 20 mm in mantle length. In adults, the mantle length continues to increase slightly faster than the head width.

The degree of prominence in the head and eyes caused problems for early workers who tried to relate small animals to adults. This feature is shown to be a larval characteristic of *T. violaceus*.

Arm Length Index (ALI).—In order to in-interpret the morphometry of the arms in terms of the ALI, the ontogeny of the arms in *Tremoctopus* must be considered. In larvae (ML 10–20 mm), arms I are the longest due to the development of long, thin filaments extending from their distal tips. The ALI of these animals reflects the development of the dorsal arm filaments. In older animals, the filaments are broken off and the truncated arms I are shorter than the arms II. The ALI is then a measure of the growth of arms II which now become and remain the longest arms.

The arm length index (Fig. 14) shows

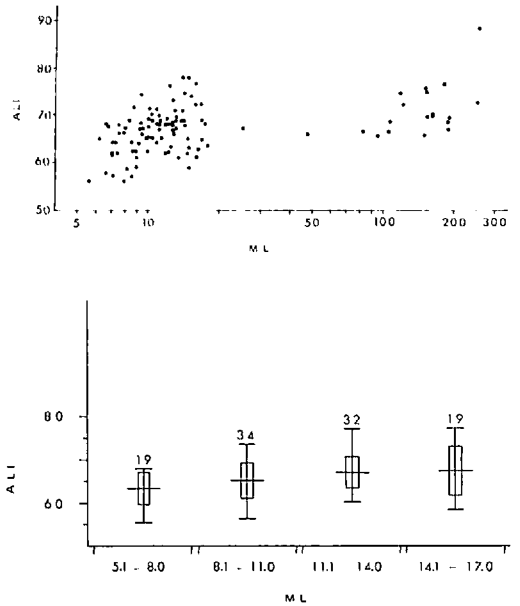


Figure 14. Arm length index plotted against mantle length in *T. violaceus violaceus* females. All are *T. violaceus violaceus*. (a, values plotted individually; b, animals grouped into size classes.)

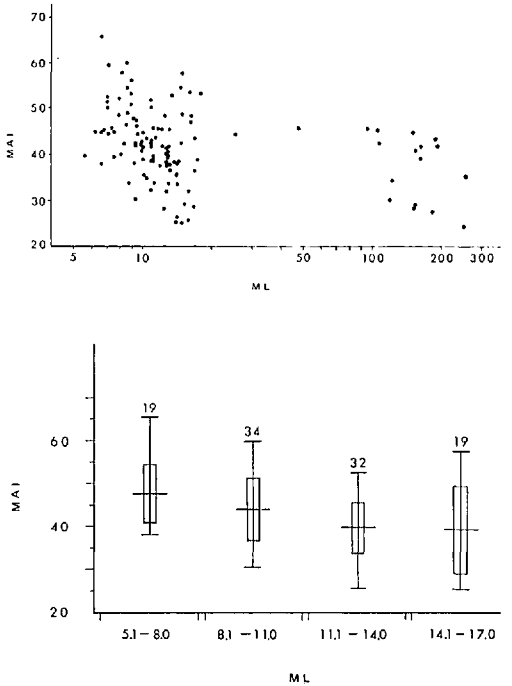


Figure 15. Mantle arm index plotted against mantle length in *T. violaceus violaceus* females. All are *T. violaceus violaceus*. (a, values plotted individually; b, animals grouped into size classes.)

considerably less variation than is found in the MWI and HWI.

Mantle Arm Index (MAI).—This measurement (Fig. 15) also indicates proportionate growth of the longest arm, although in this case it is relative to the mantle length rather than to the total length. The same problems in evaluating relative arm growth discussed above (ALI) also apply to the MAI.

The decrease in the MAI at a mantle length of about 10 mm reflects the formation of the dorsal arm filaments. The MAI increases at the stage of growth (ML about 20 mm) where the filaments are lost. In large adults (ML 200–250 mm), the MAI decreases again due to continued allometric growth of arms II.

Arm Width Index (AWI).—This index is quite constant in the animals examined although it increases slightly in the adults. Arms II are widest and the AWI indicates changes in this arm pair with growth.

Pore Length Index (PLI).—Since *T. gelatus* shows a reduction in size of its water pores, the size of the pores in *T. violaceus* relative to the mantle length (PLI) was studied (Fig. 16). There, two indices are given. The dorsal pores are usually larger than the ventral pores. In both cases, the PLI increased slightly in larger animals.

The pores are generally closed in females with a mantle length of less than about 6.0 mm but soon thereafter open to the outside, with the dorsal pores usually opening first. As the pores are capable of considerable contraction, use of the PLI as a taxonomic criterion is of dubious value.

Gill Filaments.—The Atlantic females have from 13–16 filaments on the outer demibranch of the gill. A few larvae had 12 filaments, but this low count probably re-

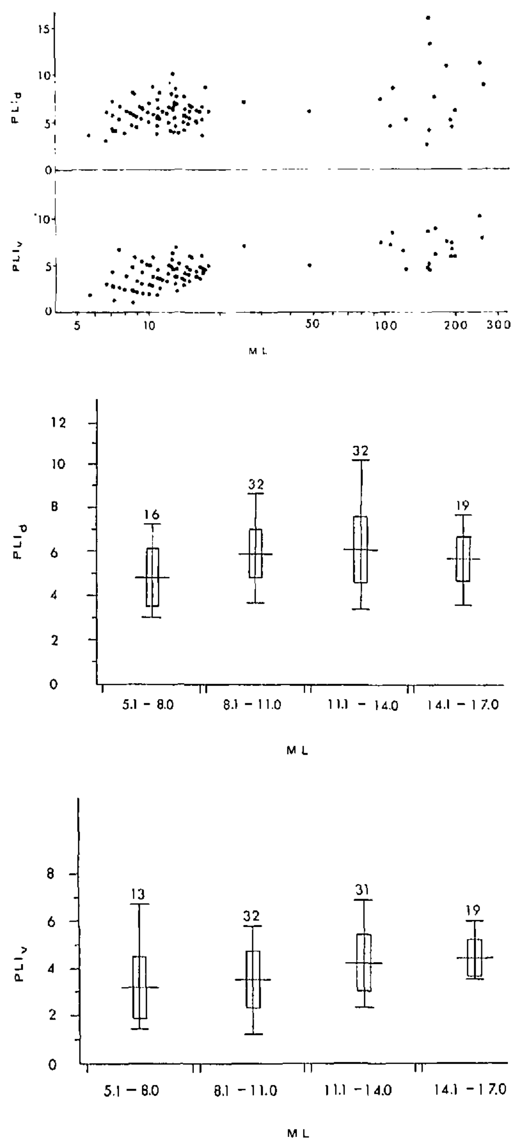


Figure 16. Pore length index plotted against mantle length in *T. violaceus violaceus* females. All are *T. violaceus violaceus*. (a, values of dorsal and ventral pores plotted individually; b, dorsal pores, with animals grouped into size classes; c, ventral pores, with animals grouped into size classes.)

flected the poor condition of the preserved animals and resulted in an uncertain gill count.

At a mantle length of about 5–7 mm, the adult number of gill filaments is already present and does not change with growth.

Funnel Organ.—The funnel organ undergoes morphological changes during the growth of the animal. Initially, it is a broad W-shaped organ with wide lateral components. This lateral portion is shorter than the medial portion of the W. The funnel organ of older animals develops several folds of glandular tissue. These folds increase in number so that when the females have reached a mantle length of about 13 mm there are often 10 or more folds of tissue on the organ. With increased size of the animals, the folds become more numerous, increase in size and begin to obscure the W-shaped base of the organ. In adult females, the funnel organ is seen as a broad transverse band of long, thin folds of glandular tissue.

Males

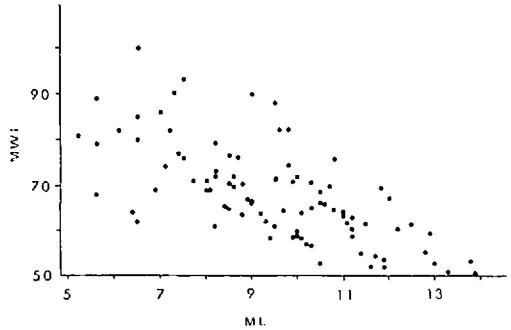
The males described here range from 5–14 mm ML. The graphs are plotted and arranged as for the females.

Mantle Width Index (MWI).—The MWI ranges from about 50%–100%. Highest values are typically found in the smallest animals and there is a trend toward decrease in relative mantle width with growth of the animal (Fig. 17). Unlike the females, this allometric growth continues to the adult stage.

Head Width Index (HWI).—Changes in this index are similar to those discussed above for the MWI. The range in HWI is 65–121%, with the smallest values in the adults.

Arm Length Index (ALI).—In males, there are no unusual changes in the structure of the arms. The ALI remains constant in all stages of growth (range 45–62%). The very long hectocotylized arm does not influence the ALI since it remains enclosed in the sac until maturity and does not enter into the measurement of the longest arm.

Mantle Arm Index (MAI).—This index also shows nearly isometric growth of the arms,



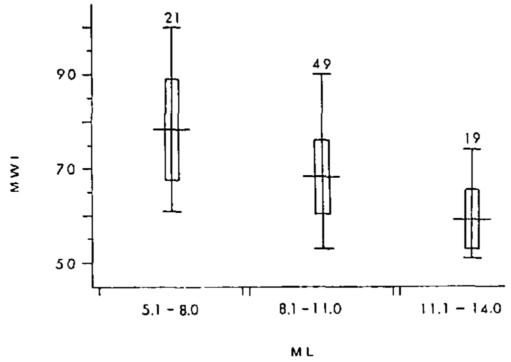


Figure 17. Mantle width index plotted against mantle length in *T. violaceus violaceus* males. (a, values plotted individually; v, animals grouped into size classes.)

in this case relative to the mantle length. The MAI shows a small range of variation in all males examined (about 45–77%).

Arm Width Index (AWI).—The width of the widest arm decreases slightly with growth.

Pore Length Index (PLI).—The discussion of the cephalic water pores of the females applies also to those of the males. The dorsal pores open first and are usually the larger of the two pairs. There is a tendency toward increasing size (relative to the mantle length) of the pores with growth.

Gill Filaments.—The number of gill filaments (9–11) in the outer demibranch remains constant during growth.

Table 2. Measurements (in mm) and indices of one female and three males of *T. violaceus* from Messina

Sex	Female	Male	Male	Male
Gill Number	13	9	10	10
ML	6.2	6.2	5.4	5.7
MWI	95.3	119.2	94.5	86.1
HWI	91.9	111.1	110.7	98.3
ALI	56.6	60.2	58.2	58.1
MAI	62.8	57.4	60.7	61.3
AWI	13.5	19.3	16.6	15.8

Tremoctopus gelatus

Because of the limited material (six females and one male), no morphometric analysis was made. It is probable that ontogenetic changes in the females parallel those of *T. violaceus*.

T. violaceus violaceus

Mediterranean (Messina)

Six males and one female from the Zoological Museum of Oslo, were loaned to the RSMAS. Measurements of four of these specimens are given in Table 2.

A comparison of the measurements in Table 2 with the data in the morphometric section indicates that the Messina animals agree well with those of the Atlantic material. The arm width index of the males is higher than in the Atlantic males, but with only three measurable males from Messina the significance of this difference cannot be determined.

T. violaceus gracilis

Hawaiian Islands

Four animals which were reported on by Berry (1912) were obtained on loan from the California Academy of Sciences (Table 3). The data agree fairly well with the morphometric data obtained from the Atlantic *T. violaceus* material, although some index values were outside the range of values. Measurements of his other ALBA-

Table 3. Measurements (in mm) and indices of nine females and five males of *Tremoctopus violaceus gracilis* from various localities in the Pacific Ocean

Station	3878	3930	3878	3929	NMFS specimens from Hawaii									
S.B. Number	218	221	218	220	HMS-30 Station 99		S10 01°27′N, 109°40′W				Okutani 20°N, 135°E			
Sex	Female	Female	Male	Male	Female	HMS-38 Female	Female	Female	Female	Male	Female	Female	Male	Male
ML	9.8	15.8	9.3	10.9	54.0	22.2	13.0	9.0	8.8	10.1	12.8	81.3	10.1	10.8
Gill Number	15	14	11	9	15	13	15	14	14	11	15	14	9	11
MWI	98.0	72.2	66.7	75.1	68.2	58.2	73.8	87.9	80.7	88.1	82.2	64.3	79.3	71.2
HWI	102.0	82.3	66.7	75.2	60.8	70.3	74.6	80.0	62.8	80.2	93.0	63.3	91.1	87.9
ALI	62.2	64.0	55.4	58.8	66.2	65.0	59.8	59.3	62.7	56.6	69.0	66.4	64.5	62.4
MAI	46.7	44.0	61.6	55.2	43.6	49.3	53.9	56.2	48.3	63.9	33.4	41.8	48.2	50.9
PLI_d	8.0	4.4	3.0	8.0	6.1	----	3.8	4.4	5.7	4.9	6.2	3.7	5.0	5.6
PLI_v	6.0	4.4	----	3.0	6.8	----	3.8	4.4	1.1	2.9	4.7	8.5	4.0	6.5
AWI	12.3	10.8	14.0	11.0	13.5	14.4	10.8	11.1	11.4	11.9	9.4	11.7	7.9	10.2

TROSS specimens can be found in Berry (1912).

Another small collection of *Tremoctopus* from the Hawaiian Islands was received on loan from the National Marine Fisheries Service in Honolulu, Hawaii. Two females, obtained from *Alepisaurus* stomach contents, are *T. gelatus* and have been discussed previously. The other three specimens are *T. violaceus gracilis.*

The two smaller females were tentatively identified by Burgess as *T. lucifer,* mainly on the basis of the brachial "light organs" (Burgess, personal communication). They should be referred to *T. violaceus gracilis.* The smaller of the two females (HMS-38) is in very poor condition and could not be measured.

Pacific Ocean

A series of 67 well-preserved animals was received on loan from the Scripps Institution of Oceanography. They were collected at 28 stations from 35°N–34°S and from 156°W–72°W.

They provided much useful morphometric information, including data on the formation of the "pouches" on the web of the adult female.

One male is a young male, *T. gelatus,* while the other animals belong to *T. violaceus gracilis* (Table 3).

Japan

Nineteen specimens from Japanese waters were loaned to RSMAS by Dr. Okutani. They include both young and adult animals, all of which are *T. violaceus gracilis* (Table 3).

Geographical Variation

T. violaceus violaceus

There is a large amount of variation in *T. violaceus violaceus.* Within a group of animals of comparable mantle lengths, indices may vary by as much as 40% (Table 4), although the range of variation is usually much less.

Large ranges in the variation of an index occur in the larvae and diminish in older animals. This can be seen in larval males and females (ML 5.1 mm–8.0 mm) where the MWI varies from 60.9–102.8%. In adults, the values range from 48.6–73.8%.

This subspecies occurs in the Mediterranean Sea, East and West Atlantic Ocean and the Gulf of Mexico. The samples obtained from near the Cape Verde Basin show no notable differences (MWI, HWI,

Table 4. Geographical variation in *T. violaceus*

Size Group (mm)	*T. violaceus violaceus* Atlantic	*T. violaceus gracilis* East Pacific	*T. violaceus gracilis* Japan
Females			
MWI			
5.1– 8.0	60.3–*80.3*–102.8	75.3–*81.9*– 89.9	
8.1– 11.0	58.2–*72.0*– 89.1	71.8–*81.0*– 93.9	
11.1– 14.0	56.8–*66.3*– 87.3	59.8–*75.6*– 91.0	61.6–*73.0*–82.2
14.1– 17.0	50.8–*62.6*– 70.8	62.9–*73.8*– 82.8	65.0–*72.2*–87.2
17.1–100.0	48.6–*57.5*– 70.2	50.7–*62.4*– 73.7	46.1–*65.8*–84.2
HWI			
5.1– 8.0	83.3–*98.7*–114.7	88.4–*93.7*–100.0	
8.1– 11.0	73.1–*90.8*–106.9	80.0–*90.4*–102.2	
11.1– 14.0	69.4–*80.7*– 90.8	74.6–*83.8*– 97.3	78.9–*86.5*–93.0
14.1– 17.0	61.9–*75.3*– 85.9	75.8–*81.8*– 90.6	77.5–*80.3*–85.9
17.1–100.0	54.2–*61.8*– 68.2	61.9–*68.6*– 78.8	59.2–*66.7*–90.6
ALI			
5.1– 8.0	55.3–*63.4*– 67.8	62.7–*63.7*– 65.2	
8.1– 11.0	56.2–*65.3*– 73.9	59.3–*67.1*– 72.8	
11.1– 14.0	60.3–*67.4*– 77.4	60.3–*69.0*– 78.7	69.0–*69.9*–70.4
14.1– 17.0	58.2–*67.5*– 77.5	59.8–*68.2*– 74.7	61.6–*65.5*–70.8
17.1–100.0	63.0–*65.8*– 67.8	61.3–*66.8*– 73.2	63.9–*66.8*–70.3
Males			
MWI			
5.1– 8.0	60.9–*78.1*–100.0	73.7–*79.0*– 83.1	
8.1– 11.0	52.9–*68.1*– 90.0	60.9–*75.4*– 99.3	71.2–79.3
11.1– 14.0	50.7–*59.1*– 73.8	57.8–*72.5*– 83.2	
HWI			
5.1– 8.0	75.3–*95.2*–121.5	83.4–*87.7*– 91.5	
8.1– 11.0	67.0–*81.7*–100.1	71.0–*80.8*– 95.5	87.9–91.1
11.1– 14.0	63.8–*71.0*– 83.1	69.8–*79.4*– 85.9	
ALI			
5.1– 8.0	55.2–*58.2*– 73.2	56.1–*57.9*– 59.6	
8.1– 11.0	46.2–*56.2*– 63.3	54.9–*59.7*– 64.2	62.4–64.5
11.1– 14.0	51.7–*56.4*– 63.3	55.4–*59.8*– 62.2	

ALI, MAI) when compared with animals from other areas within the range of the subspecies.

T. violaceus gracilis

This subspecies is widely distributed. It occurs throughout the Pacific Ocean and in the Indian Ocean. The ranges in variation of the indices are comparable to those seen in *T. violaceus violaceus.*

Animals from the East Pacific, the Hawaiian Islands and Japanese waters form a homogeneous unit. The body measurements are remarkably similar over the range of the subspecies.

T. gelatus has been collected in the Atlantic, Pacific and Indian oceans. At the present time, however, there are insufficient animals to permit evaluation of their variation.

Comparisons to Other Nominal Species

As stated previously, both females and males of *Tremoctopus violaceus* undergo considerable changes during development with larvae differing markedly from adults in their external form. Although generic characters (*viz.*, cephalic water pores) permit identification of individual larval specimens to *Tremoctopus*, until now no life history study has been made which would enable larvae to be connected with the adults.

As was indicated in the systematics sections, I consider that only two valid species of *Tremoctopus* inhabit the world oceans, *T. violaceus* and *T. gelatus*. Although 13 nominal species other than these are listed in the literature, each of these nominal species is discussed here and the reasons for its synonymy are given. Type illustrations of many of the nominal species can be found in Tryon (1879).

Tremoctopus microstomus (Reynaud, 1830)

This species was based on a specimen with a total length of 22 mm from the Atlantic Ocean (33°N, 35°W).

T. microstomus, mentioned by d'Orbigny (1840), appears to be a young *T. violaceus*. The measurements (mm) are: TL-7, ML-3, MW-3, AL-I-3, II-1, III-0.25.

In 1893, Joubin identified seven specimens (two females, five males), captured at the surface (43°33′N, 04°47′E), as *T. microstoma*. All specimens had a total length of about 25 mm. His description and illustrations show clearly that he was dealing with young *T. violaceus*.

Although Robson did not consider Reynaud's species to be a *Tremoctopus*, it is a young stage of *T. violaceus*.

Tremoctopus quoyanus (d'Orbigny, 1835)

The type locality is the Atlantic Ocean (24–26°N, 30°W). The measurements (in mm) are: TL-42; ML-12; MW-10; AL-I, 24; II, 22; III, 16; IV, 20; WD-11.

d'Orbigny's reasons for describing this as a new species included the very large head, wide body, non-truncated dorsal arms, an arm order of 1.2.4.3. instead of 2.1.4.3., and large eyes which "seem to indicate a nocturnal animal."

Hoyle (1886) assigned 17 larval specimens from the Atlantic Ocean (17°47′N, 28°28′W) to *T. quoyanus*. The largest animal had a mantle length of 12 mm. The hectocotylus was still enclosed in its sac in all males.

The dimensions of the largest female are: TL-70, ML-18, MW-16, HW-16, Sn-0.75, AL (right) I, 50; II, 45; III, 17.5; IV, 32.5.

It is interesting that Hoyle noted "it does not appear to be sexually mature and Professor Steenstrup informs me that he has never seen an individual in that condition."

Two young females (about 7 mm in mantle length) were described by Hoyle (1904) as *T. quoyanus*. These were collected in the tropical Pacific (18°19′N, 134° 57′W). Hoyle was doubtful about his identification since he observed a pattern of chromatophores not seen by d'Orbigny on the dorsal surface of the head. In other respects, such as general shape and relative lengths of the arms, the specimens agreed with d'Orbigny's description. Measurements were not given.

Tremoctopus atlanticus (d'Orbigny, 1835)

This species was described by d'Orbigny from a very small specimen (ML 4 mm). It was taken in the Atlantic Ocean (24°S, 30°W). The measurements are TL-15, ML-4, MW-4, AL-I, 10; II, 5; III, 1; IV, 3.

d'Orbigny suspected that this species might be shown in the future to represent a young stage of *T. violaceus*, although the dorsal arms are somewhat long for larval forms of *T. violaceus*.

Hoyle (1886) placed six females and eight males from the North Atlantic under *T. atlanticus*. These were all very small animals of 2.5–4.5 mm in mantle length. Neither measurements, illustrations nor descriptions were given other than to remark briefly on the length of the hectocotylus in the males.

These are probably larval forms of *T. violaceus*.

Chun (1914) listed nine specimens of *T. atlanticus* from the MICHAEL SARS material. Both Hoyle and Chun apparently based their identification on d'Orbigny's description. I agree with Robson that this species is a young form of *T. violaceus*.

Tremoctopus semipalmatus (Owen, 1836).

This species is based upon three specimens from sargassum weed in the Atlantic Ocean (30°31'N, 44°07'W). Measurements of the largest specimens are: TL about 35 mm, ML about 12 mm, HW-12 mm, number of gill lamellae-15.

Robson stated that Owen's species "has the general appearance of a young *violaceus*, but (a) its very prominent and subpedunculate eyes and (b) the relative sizes of the arms do not agree with those of *violaceus* of equivalent size."

The subpedunculate eyes were probably due to injury and, as shown in the morphometric section, the arm lengths of young *T. violaceus* exhibit a great deal of variation. Owen's good description leaves no doubt as to the identity of these specimens as *T. violaceus*.

Tremoctopus hyalinus (Rang, 1837)

This species is based upon a small specimen (total length 25 mm). It differed from the other species mainly in its large and subpedunculate eyes. Its conspicuous transparency is unlike that of *T. violaceus*, and would seem to indicate an affinity with *T. gelatus*. Water pores were neither figured nor mentioned. As neither gill counts nor measurements were given, the status of this specimen is difficult to ascertain; it might be a larval female of *T. gelatus*.

d'Orbigny agreed with Rang's description, but remarked that Rang neglected to observe the aquiferous pores. He did not give any measurements and did not see any examples of this species. His illustration was taken from Rang.

Joubin (1900) next mentioned *T. hyalinus* based on a specimen (in poor condition) taken from a fish stomach in the Azores. Joubin thought that the unusual arm formula was possibly caused by deterioration of the animal. Robson examined Joubin's specimen and concluded that it was probably an *Eledonella*. The measurements are: TL-26, ML-16, MW-14, HW-11, AL-I, 9; II, 8; III, 10; IV, 8; sucker diameter-1.

Chun (1914) examined one specimen with a dorsal mantle length of 4.5 mm and a head and mantle width of 5 mm and assigned it to this species. The features, including an arm formula of 1.2.4.3., indicate that this animal is a young *T. violaceus violaceus*.

We are dealing here with possibly three species. Those of Rang and Joubin differ strikingly from *Tremoctopus* and are perhaps larval forms of other genera. Chun was looking at either *T. violaceus* or *T. gelatus*, but which must remain uncertain.

Tremoctopus koellikeri (Verany, 1851)

Measurements (mm) given by Verany of one specimen are: TL-22, ML-8, MW-7, HW-6, AL-I, 11; II, 8; III, 3; IV, 4.

This is a juvenile of *T. violaceus*.

Tremoctopus gracilis (Eydoux and Souleyet, 1852)

The type (ML 6 mm) was from the Pacific Ocean (08°N, 106°W). Robson hesitated from synonymizing this species with *T. violaceus* because of differences in the development of the web and the relative lengths of the first and second pairs of arms.

Hoyle (1886) reported on one larval male from the Pacific. He could not place this specimen in any of the previously described species, but said that: "It appears to agree fairly with the form described by the naturalists of the BONITE, although their diagnosis is by no means so complete as might have been wished."

The dorsal arms of Hoyle's animal are about twice as long as the mantle, the ventral

arms about equal to the mantle length, and the third arm about half as long as the ventral pair.

Both pairs of water pores are present. The eyes are large, but not pedunculate as shown by Eydoux and Souleyet. These measurements conform to *T. violaceus* larvae of a similar size.

Tremoctopus dubius (Eydoux and Souleyet, 1852)

The identity of this very immature (ML 3 mm) and inadequately described specimen cannot be ascertained with certainty. It should be considered a *species dubium.*

Tremoctopus ocellatus Brock, 1832

This species is characterized by its possession of long dorsal arms, a shallow web and two ocelli located on the dorsum between the eyes. These differences are not sufficient to retain this as a distinct species.

Tremoctopus doederleini (Ortmann, 1888)

This species was based upon a female (Tokyo Bay) with a ventral mantle length of 200 mm. The measurements (mm) are as follows: TL-650, VML-200, MW-170, HW-90, AL-I, 390.

The arm formula, suckers, web and mantle sculpture show that this is not a *Tremoctopus*, but is an *Ocythoe*, perhaps *O. tuberculatus*. The two "water pores" on the dorsal surface do not appear to correspond to the true water pores of *Tremoctopus*.

Tremoctopus hirondellei (Joubin, 1895)

Joubin's single specimen (44°28′56″N, 46°48′15″W) is a very young animal with a mantle length of only 5 mm. The web is unlike that seen in a young *T. violaceus*. The arms are also unusually short. Measurements of Joubin's specimen (mm) are: TL-9, ML-5, MW-6, HW-6, AL-I, 4; II, 3.5; III, 3.5; IV, 3.5. It is possible that this animal belongs to another genus, perhaps *Argonauta* or *Ocythoe*.

Tremoctopus scalenus (Hoyle, 1904)

The body was mutilated and its shape could not be accurately determined. The head is small, with prominent eyes; the water pores could not be seen due to the damaged condition of the head. Measurements (mm) are as follows: TL-120, ML-17, AW-9, MW-0.5, AL (right)-I, 40; II, 100; III, 50; IV, 25.

I agree with Robson that this is not a *Tremoctopus*, but is probably a member of the Octopodidae, perhaps *Octopus macropus*. Since the specimen is so mutilated, its identity cannot be determined.

Tremoctopus lucifer (Akimushkin, 1963)

Akimushkin's species differs from the other species chiefly in the presence of light organs along the dorsal arms of the females. Similar organs are, however, found in females of *T. violaceus* of comparable size, and histological studies showed that these organs do not function as photophores, since a lens, reflecting layer or other structure typically associated with light organs is absent. They are probably secretory structures.

Although Akimushkin considered *T. lucifer* to be a much smaller species than *T. violaceus*, he was looking at larval and juvenile animals. *T. lucifer* is a young form of *T. violaceus*.

Conclusions

Several of the nominal species can immediately be disposed of, either as belonging to another genus or as being insufficiently characterized. As for the nominal species which should be placed in the genus *Tremoctopus*, most are clearly very young stages of *T. violaceus* and have been named without considering the ontogeny of the species.

Drastic ontogenetic changes are fairly common among cephalopods, especially among the Decapoda, and many animals once thought to represent distinct species are now known to be growth stages of other species (e.g., the "rhynchoteuthis" stage of

ommastrephids and the larval forms of cranchiids).

As seen in the morphometric section, juveniles of *T. violaceus* undergo striking changes during growth. The true nature of these nominal species can be seen by looking at a complete series of specimens.

The present study provides documentation that the nominal species of *Tremoctopus* belong to *T. violaceus*. The new species, *T. gelatus*, has not been previously described under a different name. The closest resemblance is with *T. hyalinus* (Rany), but his species must be considered a *nomen dubium*.

General Biology

Vertical Distribution

Most pelagic cephalopods undergo diurnal migrations as was first noticed by d'Orbigny (1841), who remarked that cephalopods are seen at the surface at night but descend to deeper water during the day. He also noted (1840) that his specimens of *Tremoctopus* were found at the surface where *Physalia, Glaucus* and *Janthina* were also seen. A detailed discussion of the bathymetric distribution of cephalopods and of the difficulties involved in interpreting capture data is given by Voss (1967).

T. violaceus is an inhabitant of surface waters. Nearly all of the specimens have been taken at the surface. Few captures have been made during daylight hours. The migration from the surface during the day is probably limited to about 100 m (Voss, 1967) and the vertical distribution most likely does not extend below the thermocline.

Adult females of *Tremoctopus gelatus* are known at the present time only from strandings. Anatomical features suggest that this species inhabits waters of the mesopelagic or bathypelagic zone. This conclusion is strengthened by the presence of a reduced ink sac (relative to *T. violaceus*) and by the enlargement of the eyes, features which are commonly found in deep-water cephalopods. The Florida strandings may have resulted from brief periods of upwelling which occur to a limited extent along the east coast of Florida.

Young females were collected from stomach contents of the mesopelagic fish, *Alepisaurus ferox*. The male of *gelatus* was taken at the surface at night with a light and dip net. It possessed *Physalia* fragments on the arms as in *T. violaceus*, indicating that its occurrence at the surface was not accidental.

Geographical Distribution

The animals examined in this paper were collected from the Atlantic, Pacific, and Indian oceans, and the Mediterranean Sea (Fig. 18). It can be seen that *T. violaceus* is circumtropical. *T. violaceus gracilis* occurs in the Pacific and Indian oceans; *T. violaceus violaceus* is restricted to the Atlantic Ocean, Gulf of Mexico, Caribbean Sea, and the Mediterranean Sea. Its latitudinal limits are influenced by temperature fluctuations. Few collections of *T. violaceus* are accompanied by surface temperatures at the collecting stations, but for the Discoverer material the temperatures at the surface were between 25.2°C–25.5°C.

T. gelatus is at present known from four localities: western Atlantic Ocean, Indian Ocean, and the central and eastern Pacific Oceans.

Associations With Other Animals

A conspicuous association of pelagic invertebrates, in particular coelenterates and mollusks, occurs in surface waters of the tropical Atlantic Ocean. The coelenterates include the siphonophore genera *Physalia, Porpita* and *Velella*; the mollusks include several species of the gastropod *Janthina* and the nudibranch *Glaucus*.

Early researchers (Jatta, 1896; Joubin, 1893; Naef, 1923) and later (Jones, 1963) noted that arms I and II in *Tremoctopus* contain small fragments of coelenterate tentacles, firmly held to the arms by the arm suckers. In 1963, Jones was "stung" by *Tremoctopus* while netting and handling young animals. This was due to the dis-

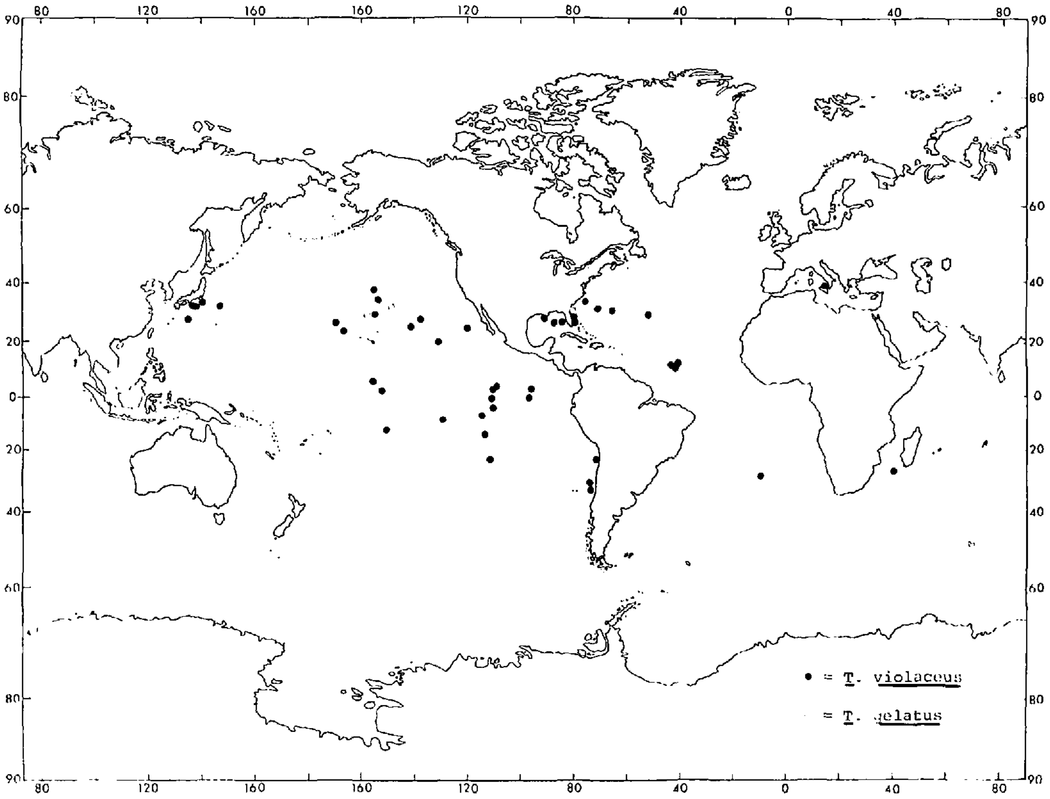


Figure 18. Map showing localities of examined specimens of *T. violaceus* and *T. gelatus*.

charge of nematocysts from *Physalia* fragments and showed that nematocyst batteries remain undischarged and may serve as a powerful potential defense mechanism. The fragments are in two rows that correspond to the two rows of suckers. They were not observed to be held by the suckers of the other arms. Occurrence of *Physalia* tentacles on *Tremoctopus* depends on the size of the octopus (90% maximum in small animals). From 77 to 90% of females with a mantle length of 5–15 mm carry *Physalia* tentacles. The percentage drops to 45% at 19 mm and none were found in larger females. In males with mantle lengths from 5–15 mm, 75 to 100% carried *Physalia* tentacles or nearly 100% of all adult males. *Physalia* fragments are found on both young and adult males, but are absent from adult females.

The functional significance of this association is not known. It is tempting to conjecture that young *Tremoctopus* actively seeks out *Physalia* for use in defense and food capture. The restriction of the tentacle fragments to arms I and II indicates that the encounter may not be accidental. It is a matter of conjecture, at this time, whether the fragments aid in food capture or serve as a defensive mechanism for the young animals.

The occurrence of *Physalia* tentacles on only young females suggests an additional hypothesis. Perhaps adult females are no longer in need of this added protection against predators or means of catching food or possibly adults do not come in contact with the siphonophores. Unfortunately, these statements will remain conjectures un-

til appropriate field and laboratory studies are conducted.

Behavior

One adult female was captured alive and observed for a short time in captivity. This animal was taken in the surf at Key Biscayne, Florida, and brought to the laboratory where it was placed in a 1,500-l tank with running seawater. After a recovery period, the animal began to swim at the surface using the second pair of arms and web. The animal soon became trapped in a corner of the aquarium and was unable to change its direction. During this time, arms I remained rolled up near the mouth.

The female was particularly responsive to tactile stimulation of the dorsal surface of the mantle; it responded by moving arms I to the posterior tip of the mantle and then by sweeping them forward over the mantle as though to remove the irritant. This response closely resembles the feeding response of *Argonauta* as described by Young (1960). This behavior was occasionally also accompanied by a 360° vertical rotation of the animal.

Reproduction

The transfer of the ripe spermatophore from Needham's sac to the tip of the hectocotylized arm and subsequently to the mantle cavity of the female has not yet been observed. Nevertheless, sufficient information, based on dissection of preserved males, is now available to permit discussion of these phenomena.

A single spermatophore is produced by the male and is stored in Needham's sac. This blind sac lies ventrally in the visceral mass and near the base of the left gill. When the hectocotylized arm uncoils, it apparently reaches into the mantle cavity through an opening in the surrounding pouch and makes contact with the visceral mass. The tissue covering the viscera is ruptured and Needham's sac is pulled through the opening that is formed.

The mechanism by which the spermatophore becomes deposited at the tip of the arm is not known. In immature males, the arm tip is spatulate, with a distally located penial filament. The flattened arm tip then folds back over itself, bringing the penial filament away from the distal region of the arm. Naef (1923) suggested that the spermatophore entered the reservoir thus formed either through its tip or through the penial filament. The function of the filament is not clear; it might be involved in later transfer of the sperm to the oviducts.

The hectocotylus of *Tremoctopus* is autotomous; it detaches at mating and remains within the mantle cavity of the female. It is not known how this exchange takes place. A few workers have described the hectocotylus as "swimming actively in search of the female" (Lane, 1960). It was also suspected by some that the male is parasitic (Lane, 1960) and remains with the female. With regard to *Argonauta,* males are commonly collected independently of females. This is also the case with *Tremoctopus.*

According to Robson (1932), calcareous secretions are embedded in the web and serve as sites for the attachment of the egg clusters. Presumably, the eggs are brooded on the web until they hatch (Portmann, 1952).

Food and Feeding

d'Orbigny (1840) examined the stomach contents of his young animals and found abundant shells of pteropod mollusks. He felt that these constituted the major food source of *Tremoctopus.* My examination of the stomach contents of adult females revealed that the adults feed chiefly on small fish.

Summary

1. Two species of *Tremoctopus* occur in warm waters of the world oceans: *T. violaceus* and *T. gelatus.*
2. *T. gelatus* is circumtropical. *T. violaceus* contains two subspecies. *T. violaceus*

violaceus occurs in the Mediterranean Sea, Atlantic Ocean and Gulf of Mexico. *T. violaceus gracilis* is found in the Pacific and Indian oceans.
3. *T. violaceus* is muscular and heavily pigmented. It is thought to be limited to the top 100 m of the water column.
4. *T. gelatus* has gelatinous tissues, enlarged eyes, a reduced number of gill filaments and a small number of chromatophores. I believe that it is a meso- or bathypelagic animal.
5. Most of the nominal species of *Tremoctopus* are growth stages of *T. violaceus*. Several nominal species belong to other genera. This is substantiated by the detailed morphometric analysis of *T. violaceus violaceus*.
6. The structure and function of the male reproductive system is described for the first time. The structure of the mature spermatophore is described and illustrated. The means of transfer of the spermatophore from Needham's sac to the hectocotylized arm is unknown.

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